OXFORD

second edition

zoo
animals

behaviour, management, and welfare

geoff hosey • vicky melfi • sheila pankhurst

Zoo
Animals

This page intentionally left blank

Zoo Animals

Behaviour, Management, and Welfare

2nd Edition

Geoff Hosey
University of Bolton

Vicky Melfi
Taronga Conservation Society Australia

Sheila Pankhurst
Anglia Ruskin University

Foreword

Zoos and aquariums[1] have a long tradition in Europe, being amongst the oldest surviving public attractions in modern day life. Many of the most famous, such as Vienna, London, and Bristol, are either fast approaching their 200th anniversary or have surpassed it. From the eighteenth century until today, people have enjoyed in their hundreds of millions the opportunity to see wild animals from far-flung places in real life—from animals that they have been familiar with since childhood through story books, to animals they have never even heard of and that seem quite fantastical. Who would not be awed by a tiger as it roars or puzzled by the wonder that is an aardvark? In our media-savvy age, with images of animals beamed from their wild habitats, there is something about seeing a real animal that is always different. Despite the wonders of institutions such as the BBC in helping us all to gain an awareness of wildlife, to truly get a sense of scale, movement, colour—well nearly everything—it helps to see the real animal.

But the professional modern zoo provides far more than a simple day out to see unusual creatures. It provides our mostly urban communities with an opportunity to see nature in a conscious way, to tap into a little of the wild, and to marvel at and value the amazing diversity of animal (and plant) life on our planet. In a recent article, the philosopher and writer Alain de Botton, noted that 'Among other things, the point of zoos should be to give us perspective on ourselves, to push us towards an awareness—always under threat in daily life—of the diversity, mystery, scale, age and complexity of the earth.' He eloquently encapsulates this somewhat hidden role that zoos play in the spiritual aspects of human life, but ask zoo visitors about the animals they have seen, and the language is often about feelings and emotions. They can connect emotionally with the animals they have seen, even if their only goal was a 'good day out'.

We are presently in the lower foothills of the United Nations Decade of Biodiversity, with its twenty targets for 2020, the so-called Aichi Targets. Target One is, at first sight, quite straightforward: 'By 2020, at the latest, people are aware of the values of biodiversity and the steps they can take to conserve and use it sustainably'. But who is going to do this? By people do we mean everyone—and how is this to be measured? Professional zoos have, of course, been talking to their visitors for decades, either via signage or face to face, about the 'value' of biodiversity and why we should save it, but in general zoos need to become better at evaluating how well this message has been getting across and finding ways to improve it—without zoos there will be a big gap in achieving Aichi Target One and therefore zoos should take on this challenge more proactively via clearer evaluation.

Professional and responsible zoos now also carry out substantial conservation work in the wild, either through the provision of funds or via undertaking direct work in field projects. In addition, captive assurance populations are managed via regional associations. Both these aspects of zoo work have increased dramatically in recent years, but there is still room for improvement in the future. However, it should be noted that association zoos collectively are amongst the most significant species conservation funders in the non-governmental organization world.

This new edition of *Zoo Animals: Behaviour, Management, and Welfare* is a welcome addition to the literature on zoos, as it provides a comprehensive background to the history, but far more importantly, the current status of zoos, how they are run, and the complexities of the multiple roles that modern zoos

---

[1] From now on zoos refers to both zoos and aquariums.

are expected to fulfil. It tackles the entire subject areas mentioned above and provides details on many more, laying down a thorough knowledge base for students of biological disciplines, as well as being accessible to interested public readers. Indeed, junior staff new to the world of zoos would be well advised to digest this book, along with the further reading suggested in the chapters, to enable them to become more skilful in their careers and their critical thinking about the profession they have entered.

This book does not shy away from highlighting areas where zoos can improve their performance and encourages thoughtful discussion of the role of the zoo in the modern day. It most clearly, via the numerous chapters, demonstrates that zoos are complicated organisms that rely on multiple specialists to function, particularly if they are to function well. It also has woven throughout its many chapters the idea of change, of progress. Zoos, like other species, must adapt and evolve to be successful, and some have been better at this than others.

Zoos are a part of the lives of tens of millions of people each year and this book delivers an insight into the world of zoos—I hope it is widely read and enjoyed.

Dr Lesley Dickie
Executive Director,
European Association of Zoos and Aquaria
November 2012

About the authors

Geoff Hosey was principal lecturer in Biology at the University of Bolton until his retirement in 2005 and is now an honorary professor at the University. He has a long-standing interest in zoo animals and, particularly, in how their behaviour is affected by the zoo environment. In addition to undertaking his own research, he has also supervised numerous undergraduate and postgraduate research projects on zoo animals. Geoff is an Associate Member of BIAZA and a member of the BIAZA Research Group. He has a keen interest in all animals, but a particular affection for lemurs—especially ringtailed lemurs *Lemur catta*.

Vicky Melfi is Behavioural Biologist with the Taronga Conservation Society Australia, based at Taronga Zoo, Sydney. Vicky started working as a zookeeper when she was 16 years old and, with the benefit of this experience and subsequent academic training, she led the behavioural husbandry and animal welfare group for the Whitley Wildlife Conservation Trust based at Paignton Zoo Environmental Park for ten years, before moving to Australia. Other than engaging in the academic duties of conducting and supervising research on the living collections at Taronga Zoo and Taronga Western Plains, Vicky also actively participates in a conservation programme to save Sulawesi crested black macaques (Selamatkan Yaki).

Sheila Pankhurst is Head of the Department of Life Sciences at Anglia Ruskin University in Cambridge, and a member of the BIAZA Research Group from 2004 to 2012; she is also an Associate Member of BIAZA. As a postgraduate student at Cambridge University, she carried out her PhD research at Whipsnade Wild Animal Park in Bedfordshire, investigating the social structure of a large South American rodent, the mara *Dolichotis patagonum*. She went on to supervise further research into the ecology and parasitology of the mara (in collaboration with the Zoological Society of London), and has also supervised many undergraduate projects at zoos. Sheila has had a special interest in rodents, from all taxonomic groups, since she was a very small child.

This page intentionally left blank

Preface and acknowledgements

Welcome to the second edition. It is four years since the first edition appeared, and in that time we have been delighted by the warm reception that this book has received, both in the zoo profession and in colleges and universities. The book is now prominent on many course reading lists, and, we're proud to say, it is also to be found on many a zoo professional's bookshelf. But zoo biology moves on, and a number of important studies have been published in the last four years which have advanced both the theory and practice of zoo animal management. Central to this has been an increasing appreciation, at least in the better zoos, of the need for zoo practice to be evidence-based, drawing on empirical studies published in the peer-reviewed literature.

This book is about that evidence base, and what it tells us about the behaviour, management, and welfare of animals in zoos. And, of course, that evidence is best understood within its context, so we also consider aspects of the context within which zoos operate, such as their history and their role in conservation and education. Equally important to this book is consideration of how that evidence base comes about through the application of scientific research methodology.

In the four years since the first edition of this book appeared, several other books have been published on zoo science, including the second edition of the mighty and authoritative *Wild Mammals in Captivity* (Kleiman *et al*. 2010). We welcome all of these (though naturally we think ours is the best!); zoo biology is a growing area, but one which has been relatively neglected in the textbook arena, so it is encouraging to see it becoming a recognized branch of science. So our main aim in producing this second edition is to update the information we presented in the first edition to take account of the many excellent new studies that have been published since, and hopefully to continue to provide a comprehensive and stimulating account of modern zoo biology which will be of interest and use to students, their supervisors, zoo professionals, and zoo enthusiasts alike. There really is nothing quite like getting close to animals, and if possible working with them, as the continued popularity of zoos attests. People want to visit zoos, to work in them, and to do research in them, and hopefully this book will help make these experiences even more enjoyable, whilst ensuring that the welfare of the animals remains the highest priority. Between the three of us, we have clocked up more than 60 years of researching in, working in, and supervising students in zoos. We hope that this, together with the particular mix of zoo-based and university-based experience that we have, makes us a strong team for writing this book.

We received a great deal of positive feedback after the first edition of *Zoo Animals* from reviewers in the scientific journals, from readers online, from anonymous reviewers, and informally from colleagues and students we have met at various universities, conferences, and zoos. Our thanks go to all of them, and we have tried to take note of all of their comments in our updating of this book.

We were fortunate for the first edition in having many colleagues who were willing to read and make constructive (and often critical) comments on various drafts of chapters, and their input improved the book immeasurably. Their influence is still apparent in this second edition, and, of course, it goes without saying that any errors or omissions that remain in the book are our responsibility and not theirs. But many colleagues have also provided us with help and information for this second edition. In particular, we warmly thank Andrea Fidgett and Stephanie Sanderson (Chester Zoo), and Miranda Stevenson at BIAZA, who have helped us to understand the intricacies of zoo animal nutrition and health, and the legislative framework within which zoos operate, as well as providing encouragement and support

Contents

List of boxes

List of acronyms

(See also Glossary)

Note: UK, USA, or Australia in parentheses after an entry denotes the country of origin for legislation, government departments, etc.

AArk	Amphibian Ark
AAZK	American Association of Zoo Keepers
AAZPA	American Association of Zoological Parks and Aquariums *(Now the AZA—see below)*
AAZV	American Association of Zoo Veterinarians
ABP	Animal By-Products Regulations 2005 *(UK)*
ABS	Animal Behavior Society *(USA)*
ABWAK	Association of British Wild Animal Keepers
ACTH	adrenocorticotropic hormone
ADF	acid detergent fibre
AHA	Animal Health Australia
AI	artificial insemination, avian influenza ('bird flu')
AKAA	Animal Keepers Association of Africa
ALPZA	Latin-American Zoo and Aquarium Association
ANCMZA	Advanced National Certificate in the Management of Zoo Animals *(UK)*
ANOVA	analysis of variance
APHIS	Animal and Plant Health Inspection Service *(Part of the US Department of Agriculture)*
APP	African Preservation Programmes
ARB	abnormal repetitive behaviour
ARKS	Animal Records Keeping System
ART	assisted reproductive technology
ASAB	Association for the Study of Animal Behaviour *(UK)*
ASG	Amphibian Specialist Group
ASZK	Australasian Society of Zoo Keeping
ATA	Animal Transportation Association
AV	approved vet
AWA	Animal Welfare Act of 1966, as amended *(USA)*; Animal Welfare Act 2006 *(UK)*
AZA	Association of Zoos and Aquariums *(Formerly the AAZPA—see above. The organization changed its name first to the American Zoo and Aquarium Association in 1994; (there is no 'American' in the current title.)*

BAP	Biodiversity Action Plan *(UK)*
BIAZA	British and Irish Association of Zoos and Aquariums
BIS	Department for Business, Innovation, and Skills (*UK*)
BMR	basal metabolic rate
BSE	bovine spongiform encephalopathy
BVA	British Veterinary Association
BVS	BSc in Veterinary Surgery
BVZS	British Veterinary Zoological Society
CAZA	Canadian Association of Zoos and Aquariums
CAZG	Chinese Association of Zoological Gardens
CBD	1992 Convention on Biodiversity
CBP	captive breeding programme
CBSG	Conservation Breeding Specialist Group *(Formerly the Captive Breeding Specialist Group—the name was changed in* 1994)
CCTV	closed-circuit television
CFU	colony-forming unit
CHP	combined heat and power
CITES	1973 Convention on International Trade in Endangered Species of Wild Fauna and Flora
CNS	central nervous system
CoPs	Conference of the Parties *(A country that signs up to a UN treaty or convention is known as a 'Party')*
COSHH	Control of Substances Hazardous to Health *(In relation to UK Health and Safety regulations)*
COTES	Control of Trade in Endangered Species (Enforcement) Regulations 1997 *(UK)*
CP	conservation programme
CPS	Crown Prosecution Service *(UK)*
CR	conditioned response
CS	conditioned stimulus
CSF	cafeteria-style feeding
CWD	chronic wasting disease
DCMS	Department for Culture, Media and Sport *(UK)*
DE	digestible energy
Defra	Department for Environment, Food and Rural Affairs *(UK)*
DESD	Decade of Education for Sustainable Development
DfES	Department for Education and Science *(UK)*
DNA	deoxyribonucleic acid
DTI	Department of Trade and Industry *(UK)*
EAZA	European Association of Zoos and Aquaria
EAZWV	European Association of Zoo and Wildlife Veterinarians

EC	European Community *(Confusingly, the European Commission, which is part of the EU—see below—is also sometimes referred to by the abbreviation EC)*
ECAZA	European Community Association of Zoos and Aquaria *(Now the EAZA—see above)*
EEKMA	European Elephant Keeper and Manager Association
EEP	European Endangered species Programme *(The acronym is taken from the German: Europäisches Erhaltungszuchtprogramm)*
EFA	essential fatty acid
EFSA	European Food Safety Agency
EGZAC	European Group on Zoo Animal Contraception
ELISA	enzyme-linked immunosorbent assay
ENG	EAZA *(see above)* Nutrition Group *(Formerly the EZNRG—see below)*
ESB	European studbook
ESU	evolutionarily significant unit
EU	European Union
EZNRG	European Zoo Nutrition Research Group *(Now the ENG—see above)*
FAA	food anticipatory activity
FAO	United Nations Food and Agriculture Organization
FDA	Food and Drug Administration *(USA)*
FMD	foot and mouth disease
FMR	field metabolic rate
FSC	Forest Stewardship Certificate
FSH	follicle-stimulating hormone
GAS	general adaptation syndrome
GE	gross energy
GI (tract)	gastrointestinal (tract)
GnRH	gonadotropin-releasing hormone
GRB	genetic resource bank
GSMP	global species management programme
HPA/G (axis)	hypothalamo-pituitary-adrenal/gonadal (axis)
HSE	Health and Safety Executive *(UK)*
IATA	International Air Transport Association
ICEE	International Conference on Environmental Education
ICEE	International Conference on Environmental Enrichment
ICSI	intracytoplasmic sperm injection
ICZ	International Congress on Zookeeping
ICZN	International Commission on Zoological Nomenclature
ISAE	International Society for Applied Ethology
ISIS	International Species Information System
ISO	International Organization for Standardization
IUCN	International Union for the Conservation of Nature

IUDZG	International Union of Directors of Zoological Gardens
IVF	*in vitro* fertilization
IZW	Leibniz Institute for Zoo and Wildlife Research
JMSP	Joint Management of Species Programme
JNCC	Joint Nature Conservation Committee *(UK)*
LARs	IATA *(see above)* Live Animal Regulations
LH	luteinizing hormone
MBA	Methods of Behavioural Assessment
MBD	metabolic bone disease
ME	metabolizable energy
MedARKS	Medical Animal Records Keeping System
MHC	major histocompatibility complex
MHSZ	*Managing Health and Safety in Zoos*
MK	mean kinship
MSW	Mammal Species of the World
mtDNA	mitochondrial DNA
MTRG	Marine Turtle Research Group
MVP	minimum viable population
NAG	Nutrition Advisory Group *(of the AZA—see above)*
NAP	National Academy Press
NDF	neutral detergent fibre
NGO	non-governmental organization
NRC	National Research Council *(USA)*
NSAID	non-steroidal anti-inflammatory drug
OIE	Office International des Epizooties *(Also known as the World Organisation for Animal Health)*
PAAZAB	African Association of Zoological Gardens and Aquaria *(Formerly the Pan-African Association of Zoological Gardens and Aquaria, from which title the acronym's initial 'P' remains)*
PETA	People for the Ethical Treatment of Animals
PFA	pre-feeding anticipation
PhD	Doctor of Philosophy degree *(A higher degree than a BSc or MSc)*
PIT	passive integrated transponder
PMP	population management plan
POE	post-occupancy evaluation
PRL	prolactin
PRT	positive reinforcement training
PSM	plant secondary metabolite
PVA	population viability analysis
RAE	Research Assessment Exercise *(UK)*

RCP	EAZA *(see above)* Regional Collection Plan
RCVS	Royal College of Veterinary Surgeons *(UK)*
REEC	Regional Environmental Enrichment Conferences
RIA	radio-immunoassay
RSG	Reintroduction Specialist Group
RSPB	Royal Society for the Protection of Birds *(UK)*
RSPCA	Royal Society for the Prevention of Cruelty to Animals *(UK)*
SAZARC	South-Asian Zoo Association for Regional Cooperation
SDB	Self-directed behaviour
SHEFC	Scottish Higher Education Funding Council
SIB	self-injurious behaviour
SPARKS	Single Population Analysis and Records Keeping System *(SPARKS is a studbook management system)*
SPI	spread of participation index
SPRG	Scottish Primate Research Group
SSC	IUCN *(see above)* Species Survival Commission
SRP	species recovery programme *(UK)*
SSP	species survival plan
SSSMZP	Secretary of State's Standards of Modern Zoo Practice *(UK)*
SUZI	sub-zonal insemination
SVL	snout–vent length
SVS	State Veterinary Service
TAG	Taxon Advisory Group
TB	tuberculosis
TCF	Turtle Conservation Fund
TPR	temperature, pulse, and respiration
TRAFFIC	*Note that TRAFFIC is not an acronym, but rather the proper name of an organization*
TSE	transmissible spongiform encephalopathy (e.g. BSE—*see above*)
TWG	Taxon Working Group *(UK)*
UFAW	Universities Federation for Animal Welfare
UNCED	United Nations Conference on Environment and Development
UNEP	United Nations Environment Programme
UNFCCC	United Nations Framework Convention on Climate Change
UR	unconditioned response
US	unconditioned stimulus
USDA	US Department of Agriculture
UV	ultraviolet
WAZA	World Association of Zoos and Aquariums
WCC	AZA Wildlife Contraception Center
WCS	Wildlife Conservation Society *(Based in New York)*

WIN	Wildlife Information Network
WLCA	Wildlife and Countryside Act 1981 *(UK)*
WNV	West Nile virus
WWF	Formerly, the World Wide Fund for Nature—now known only by the acronym
WZACS	World Zoo and Aquarium Conservation Strategy
WZCS	World Zoo Conservation Strategy
ZAA	Zoo and Aquarium Association
ZEC	Zoos Expert Committee
ZIMS	Zoological Information Management System
ZLA	Zoo Licensing Act 1981 *(UK)*
ZOO	Zoo Outreach Organisation
ZSL	Zoological Society of London

Chapter 1
Introduction

It has been estimated that, throughout the world, there are something like 10,000 animal collections that come under the general heading of zoos (Gusset and Dick 2011). We do not know how many visitors they all receive annually, but it is certainly in the order of at least hundreds of millions. Of these zoos, about 1,200 belong to regional or national associations, which endeavour to foster cooperation and to ensure high professional standards among their members. These 1,200 **accredited zoos** alone receive more than 700 million visits every year (Gusset and Dick 2011), which makes going to the zoo one of the most popular leisure pursuits across the world. In North America, it is often said that zoos attract more visitors than professional baseball, basketball, and football games combined. In the UK and Ireland, more than 23 million people visited accredited zoos in 2008, which is one in three of the population (BIAZA 2010a).

So what do these statistics tell us? Firstly, they suggest that the motivation to see, at close hand, real live **exotic animals** is very strong among people. But they also indicate that the worldwide zoo community can have real influence in shaping people's attitudes towards, and knowledge of, animals. This, in turn, can result in more public concern and support for raising welfare standards and promoting conservation. Zoos are in an ideal position to capitalize on this.

Modern zoos are no longer only places that keep a few animals for people to go and look at. They are scientifically run and governmentally regulated institutions, which have a significant role to play in our relationship with the natural world. Many zoos describe their role in terms of four key words: conservation, education, research, and recreation. These roles have been defined more precisely in the last two decades, and this has been accompanied by a great increase in knowledge about the needs of animals and the best ways of maintaining them in captivity. In this book, we review and synthesize much of this knowledge to provide an overview of the functions and operations of modern zoos, how they manage their animals, why they keep them in the way that they do, and how they try to provide environments that ensure the best welfare of the animals. Our philosophy in writing this book is that the management of zoo animals needs to be evidence-based, with most of that evidence coming from the best scientific research in peer-reviewed journals (Melfi 2009). We use this evidence here to try to show what is currently regarded as best practice in accredited zoos, and the knowledge and scientific research on which that best practice is based.

1.1 Who is this book for?

The short answer to the question of who this book is for is that we hope that there will be something of use and value in here for anyone who has an interest in zoos and the animals they keep.

However, we did have two particular groups of people in mind when preparing this book. Firstly, we have tried to provide an up-to-date overview of zoos and zoo-related issues for the keepers, vets,[1] curators, education officers, and other zoo professionals who look after exotic collections. These people are highly knowledgeable specialists in their own particular field, but may want to know more about other aspects of how modern zoos work. The second group that we had in mind is the growing body of college and university students who study zoo animals as part of their course, and who will almost certainly visit a zoo at some stage in their studies to observe and learn about its animals. Courses that include a consideration of zoo animals have proliferated over the past 10 years, and are often to be found with titles such as 'Animal Management', 'Animal Behaviour', 'Animal Welfare', 'Conservation', and a variety of other terms. There has previously been no readily accessible text covering the biology of zoo animals at an appropriate level for students on these courses. There is, of course, the classic and excellent—but perhaps rather formidable—*Wild Mammals in Captivity* (Kleiman *et al*. 1996), now updated as a second edition (Kleiman *et al*. 2010), which synthesizes a huge amount of literature about mammals in zoos. We do not intend to compete with that tome. Our book is broader, assumes less prior knowledge, and covers birds, **herps**, fish, and invertebrates, as well as mammals.

With such a diverse intended readership, identifying the appropriate level for the book has been no easy task. Students following modules or courses that include consideration of zoo animals may be registered for particular certificates or diplomas, may be foundation or honours degree undergraduates, may be on taught masters courses, or may be beginning their studies for a PhD. Zoo professionals are likely to have one or more of these qualifications already. What we have assumed is that most readers will have a basic knowledge of biology and that, while they may have a very good understanding of one or two of the biological topics covered in this book, they may not have the same level of familiarity with all of the areas covered. This probably means that the book as a whole is located at around roughly the second and third year of an honours degree, but we say that only as a guide to its style and content; we hope that the text is not too difficult or too patronizing for those who approach it at a different level. Our feedback from users of the first edition suggests to us that we have got the level broadly right.

While we have assumed that most of our readers will already have some basic biological knowledge, biology is a very broad discipline and even professional biologists are not usually proficient in all areas of the subject. For this reason, we have included in each chapter a brief review of the relevant background theory in the hope that the rest of the chapter is intelligible to all readers regardless of their previous knowledge.

Because we are familiar with, and have been working within, the zoo animal management systems that operate in the UK and Ireland, Europe, and more recently Australasia, our perspective in this book very much reflects this orientation. However, in this second edition we have tried to give more of an international perspective, partly because (to our great delight) the book has been widely adopted in a great many countries, to reflect so much good zoo research being undertaken throughout the world, and not least because one of us (VM) now works at a zoo on the other side of the world.

---

[1] We use the abbreviation 'vets' throughout this book to refer to veterinary surgeons and scientists. The word has a somewhat different connotation in North America.

1.2 Sources of information

There is now a large literature on zoo animals. Despite this, we have become very aware in preparing this book just how many gaps there are in our knowledge. There are large areas of zoo biology that have not been empirically studied at all, and plenty of other areas in which there are very few studies. In some of these areas, we have been able to refer to studies on laboratory, farm, companion, or wild animals, but it should always be borne in mind that the zoo environment is very different from these other environments, and so we should apply such studies with caution. We have identified these gaps in knowledge wherever possible and hope that this will stimulate fresh research in future.

Although there is a large zoo literature, accessing it is not necessarily very easy. Many of the **empirical studies** about zoo animals are published in a small number of peer-reviewed journals, notably *Zoo Biology*, *Applied Animal Behaviour Science*, and *Animal Welfare*. These are usually within the full-text subscriptions of university (and some zoo) libraries, but also allow free access to abstracts of the papers on their websites. We have tried to use peer-reviewed sources wherever possible, partly because it ensures the reliability of the source, but also because they are relatively easy to access from most libraries. However, there is a substantial non-peer-reviewed zoo literature,[2] some of which contains results from empirical studies, but much of which contains only anecdotal information.

The availability of some of these sources to people outside the zoo world (and perhaps also to some of those within it) can be very poor and, for this reason, we have avoided such sources if alternative sources in the peer-reviewed literature are available. In any case, we have not undertaken exhaustive reviews of the literature in this book. Instead, we have tried to concentrate on notable papers that have advanced theory or practice, together with appropriate examples drawn from those that are available. In doing this, we have attempted to give due prominence to a range of different species, but it remains the case that a large proportion of zoo animal studies are on mammals and that, of the studies on mammals, a large proportion of these focus on primates.

As well as the works which we refer to in each chapter and which are listed in the References section at the end of the book (we thought that this would be better than having a separate references section for each chapter), we have also tried to identify, in each chapter, sources of further information and appropriate further reading. Of course, websites can come and go, and their addresses can change, so the best we can do is to provide sites that are current at the time of final writing (November 2012), and direct people to the Online Resource Centre that supports this book.

We have also added a selection of questions at the end of each chapter, and hope that these will stimulate readers to think about what they have read and that they will act as prompts for discussion of some of the issues that we raise. In general these are the same questions that we asked in the first edition; most of them still need a decent answer!

1.3 What do we mean by 'zoo'?

While the question of what we mean by 'zoo' may, at first sight, seem a rather strange question to ask, it is more than just pedantry to ask for some sort of definition of terms. As we shall see in subsequent chapters, it is important for our interpretation of animal behaviour in the zoo to be able to compare it with behaviour in other situations, and, for this, we need to know

---

[2] The non-peer-reviewed literature about zoo animals is sometimes referred to as the 'grey literature'. Examples range from the newsletters of zoo associations, such as *Lifelines* published by BIAZA, *Shape of Enrichment*, and zookeepers' journals, e.g. *Thylacinus* published by the Australasian Society of Zoo Keeping. (See **Box 14.5** for more information.)

how we can separate the zoo environment from those other situations. Furthermore, some of the research that informs our understanding of the needs of animals in zoos and the most appropriate ways of managing them has not, in fact, been done in a zoo, but may have been undertaken at some other kind of animal facility. Again, we can only start to identify ways in which these other facilities differ from zoos if we have a clear idea of what we mean by 'zoo'.

So, what is a zoo?

The UK Government, in the legislation that covers zoos, defines the zoo as:

> an establishment where wild animals are kept for exhibition (other than a circus or a pet shop) to which members of the public have access, with or without charge for admission, on more than seven days in any period of twelve consecutive months.
> Zoo Licensing Act (HMSO 1981)

Circuses and pet shops are excluded, because they are covered by other legislation, but the definition nevertheless permits the inclusion of such establishments as aquariums, butterfly houses, and safari parks, as well as conventional zoos.

Of course, this definition is driven primarily by the requirements of a legal framework, but it does not differ significantly from the view taken by other organizations within this field. For example, the World Association of Zoos and Aquariums (WAZA), in its 1993 *World Zoo Conservation Strategy* (IUDZG/CBSG 1993), does not give a formal definition of a zoo, but offers two features that characterize zoos:

- they '*possess and manage collections that primarily consist of wild (non-domesticated) animals, of one or more species, that are housed so that they are easier to see and to study than in nature*';
- they '*display at least a portion of this collection to the public for at least a significant part of the year, if not throughout the year*'.

These definitions are helpful. They allow us, for example, to include small-animal collections in museums, specialist collections, aquariums, bird parks, and the like (**Fig. 1.1**). Significantly, they exclude private and university collections that are not normally open to the public, or are only open for a handful of days each year.

Figure 1.1 Places such as (a) butterfly houses and (b) aquariums are regarded as zoos within most definitions, and come within the scope of this book if they are within recognized accreditation systems. (Photographs: (a) Geoff Hosey; (b) Jeroen Stevens)

This, then, is the concept of the zoo that we use in this book, and when we use the word 'zoo', we use it to include implicitly the aquariums and other publicly accessible collections of wild animals. Unfortunately, in ordinary everyday language the word 'zoo' is often used to denote *any* collection of animals, including privately owned menageries and small collections which are not part of any association or, in many cases, covered by any legislation. There are a large number of these throughout the world, and the standards in most of them are very poor. But in general these collections do no research, are not involved in conservation, and pay little or no regard to animal welfare. So, while we will continue to just use the term 'zoo' here, virtually all of what we have to say in this book is about, and uses information gained from, accredited zoos and aquariums.

1.4 The scope of the book

The book is about how animals are managed in zoos (their housing, husbandry, health, **nutrition**, and breeding) and also the way in which animals experience the zoo environment (their behaviour, welfare, and interactions with people). But to gain a full understanding of the zoo as an environment for animals and people, it is also useful to consider the context in which zoos operate, and their contribution to species and habitat conservation both within and beyond the zoo's boundaries. Therefore we also briefly consider legislation, conservation (both *ex situ* and *in situ*), record-keeping, and research.

Zoos have a major role to play nowadays in awareness raising and education about animals and environmental issues, and we consider this role briefly in so far as it affects the animals and their environment. This book is about zoos today and, with the exception of the brief overview of zoo history in **Chapter 2**, its content is about the health, welfare, and management of animals in modern zoos, and not about any failings in welfare provision, or health care, or husbandry, that may have occurred in the past.

We will now provide a brief summary of the content of each chapter of the book.

1.4.1 The history and philosophy of zoos (Chapter 2)

Collections of wild animals are not a new phenomenon. History records a number of private collections of animals, from the parks of ancient China to aristocratic **menageries**, including the menagerie kept at the Tower of London during medieval times. But the 'modern' zoo, in a form that we would recognize now, dates only from the end of the eighteenth century. Zoos increased greatly in public popularity during the nineteenth century, largely as places that provided entertainment and enjoyment for their visitors (even though the intention of their founders may have been the pursuit of scientific ideals).

Nowadays, we tend not to see the zoos of yesteryear as having any particular educational, scientific, or conservation role at that time, yet the two leading zoos of the nineteenth century in Europe (the Jardin des Plantes, in Paris, and London Zoo—**Fig. 1.2**) were very much scientific institutions. In any case, it is possible that, in a society that was becoming increasingly industrialized and urbanized, zoos passively helped to raise visitors' interest and awareness of the living world simply by giving them the opportunity to experience animals that would not otherwise be a part of their lives.

The history of zoos shows us the evolving context in which wild animals have been kept, and reflects changing views in both society and the zoo world. This history is considered more fully in **Chapter 2**, which concludes with a brief overview of the philosophy and **ethics** of zoos.

1.4.2 The regulatory framework (Chapter 3)

As with so many organizations, many zoos operate within a regulatory framework that includes both mandatory requirements (that is, those required by law) and procedures seen as reflecting
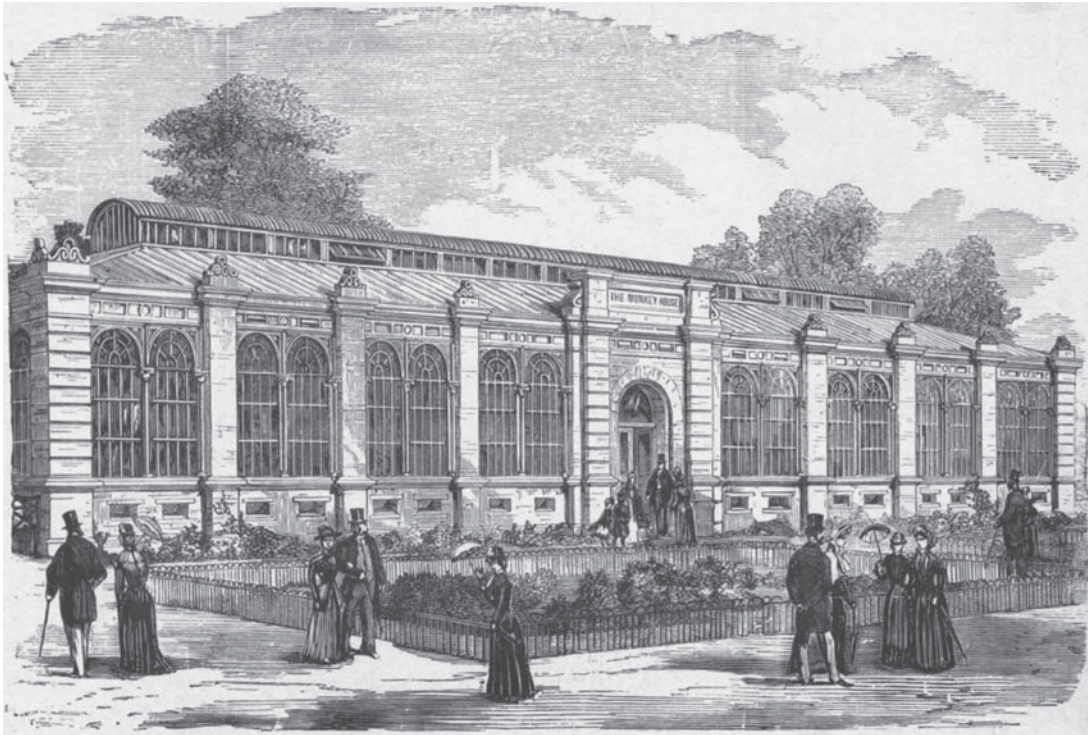
Figure 1.2 The monkey house at London Zoo in late Victorian times (from John Fletcher Porter (1980) *London Pictorially Described*). (Picture: Lee Jackson, **http://www.victorianlondon.org**)

good practice, which are stated in various guidelines and codes of practice (**Fig. 1.3**). Within the UK, the regulatory framework for zoos is stringent, and generally ensures high standards of welfare and husbandry. Similar regulatory frameworks apply to different extents in other regions of the world and these are also briefly considered in this chapter.

In **Chapter 3**, we concentrate on describing and interpreting this framework, both in the UK and, where feasible, elsewhere in the world.

1.4.3 Behaviour (Chapter 4)

Modern zoo housing and husbandry often aim to provide the animals with many of the opportunities for behaviour that they have in the wild. Nevertheless, the zoo environment can be quite different from many wild environments and, if we want our zoo animals to behave in the same

Figure 1.3 The United Nations Convention on Biological Diversity (CBD) was a major outcome of the 1992 'Earth Summit' in Rio de Janeiro, and forms the framework for much national and international legislation on the role of zoos in conservation. (Picture: Secretariat of the CBD)

Figure 1.4 This young Hamadryas baboon *Papio hamadryas* has just been chased by a more dominant animal, and is showing a submissive facial signal and body posture. Social interactions within groups are an important part of the behaviour of both wild-living and zoo-housed animals. (Photograph: Geoff Hosey)

way as their wild counterparts (**Fig. 1.4**), then we must look closely at the precise ways in which zoo environments differ from the wild and how these differences affect behaviour.

This chapter examines some of the features of zoos that influence behaviour—an area of study that is growing in research importance. It also looks critically at the notion that the 'wild' provides an appropriate benchmark for evaluating and interpreting all aspects of animal behaviour.

1.4.4 Animal identification and record-keeping (Chapter 5)

An essential part of managing collections of zoo animals is knowing your animals (**Fig. 1.5** and **Plate 1.1**) and what has happened to them in their lives. For example, a knowledge of previous health issues and veterinary treatments is important in managing an animal's future health, and a knowledge of ancestry and genetic relationships is necessary for planning **captive management programmes**.

In most zoos, the days of filing cards have long gone and animal records are maintained on computer databases. This opens up opportunities to look beyond individual zoos and to start to identify trends in whole **taxa**, so these records

Figure 1.5 Humboldt's penguin *Spheniscus humboldti* with an individual wing band to aid identification. (Photograph: Geoff Hosey)

provide a valuable research database over and above their usefulness in the day-to-day management of the animals.

The use of zoo records for research is considered in more detail in this chapter and also in **Chapter 14**.

1.4.5 Housing and husbandry (Chapter 6)

Housing for zoo animals has changed greatly over the past 150 years and it is rare nowadays—at least in the accredited zoos that are the main focus of this book—to see relatively **barren enclosures** made from concrete, iron bars, and wire. Some ideas of zoo architecture have, in the past, leant more in the direction of what looks good to the visitors rather than what is appropriate for the animals. Today, it is considered necessary to plan housing for zoo animals from multiple points of view, taking into account all the main 'stakeholders': animals, the public, and the zoo staff. This chapter considers these points of view, and examines the different kinds of housing that can be seen in zoos today.

Husbandry is about the day-to-day maintenance of the animals (**Fig. 1.6**), an area that is still very much dominated by experience rather than empirical data, and the extent of knowledge and practice in zoo husbandry is covered in the rest of this chapter.
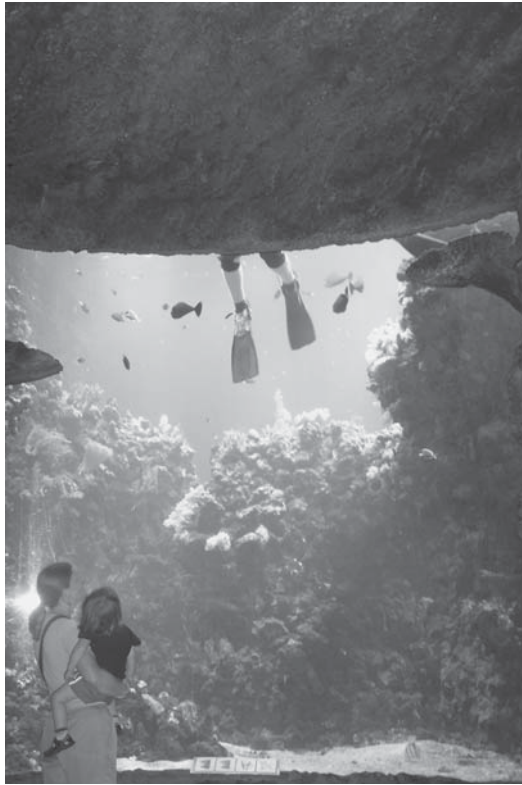
Figure 1.6 Housing and husbandry of aquariums can involve getting into the water to clean the tanks. (Photograph: Andrew Bowkett)

1.4.6 Animal welfare (Chapter 7)

Of course, zoos have changed over recent years in more than just the design of their enclosures. An increasingly detailed understanding of the physical and psychological needs of animals (**Fig. 1.7**) has led to their welfare being a priority for zoos, and this welfare priority recognizes that animals have needs over and above simply being comfortably housed and fed. There is now a large body of theory underlying our knowledge of welfare issues and, although this has largely been developed in the context of farm and laboratory animals, considerable advances have been made in zoo animal welfare as well. Amongst other aspects of zoo animal welfare, this chapter identifies the need to accentuate the positive; to explore indicators of positive welfare, as well as considering how to prevent poor welfare.

Figure 1.7 This giraffe *Giraffa camelopardalis* is showing an oral stereotypy (repetitive licking or chewing movements), which suggests that it has experienced less than optimal welfare at some point in its life. (Photograph: Vicky Melfi)

1.4.7 Environmental enrichment (Chapter 8)

In some respects, the concept of **enrichment** brings together the behaviour and the welfare of zoo animals. One of the reasons why it is considered important to encourage zoo animals to show similar behaviours to those they display in the wild is the belief that their welfare is compromised if they cannot. Enrichment aims to fill gaps in the opportunities that animals have to display their full range of behaviours (in other words, to change their behaviour—**Fig. 1.8**), and

Figure 1.8 Some enrichments are designed to make the animal spend more time in feeding and foraging, like this ice block for short-clawed otters *Aonyx cinerea*. (Photograph: Jeroen Stevens)

sometimes to change physiology or other aspects of the animal's biology. What these should be changed to is a debatable issue, which is considered in this chapter, along with descriptions of the main forms of enrichment.

1.4.8 Small population management (Chapter 9)

Previously referred to as captive breeding, managing small populations in zoos, when done correctly, can lead to good animal welfare and a positive contribution to conservation (**Fig. 1.9**). Based on a sound knowledge of reproductive biology, decisions about how to manage small zoo populations are determined by logistical, genetic, and demographic considerations. The end goal is to ensure self-sustaining zoo populations with high **genetic diversity** and low **inbreeding** (although the extent to which zoos achieve this goal is the subject of much debate and some justified criticism).

Part of this population management process might involve the use of various technologies to assist (for example, *in vitro* **fertilization**, **artificial insemination**) and monitor (for example, **ultrasonography**, **hormone assays**) reproduction, or by contrast methods to limit breeding (for example, contraception or single-sex housing). These techniques are described in this chapter,

which also considers how small population management decisions will affect the life of individuals (individual life plans), populations (cooperative management programmes), and larger groups of animals housed in zoos (regional collection plans).

1.4.9 Conservation (Chapter 10)

One of the most significant changes in zoos since their formation has been a shift towards an active role in conservation and education, rather than only the exhibition of exotic species. Human involvement in the extinction of species, through hunting and habitat destruction, goes back to prehistoric times and has been implicated in the extinction of large vertebrates in Australia, Madagascar, and the Americas. In historic times, the first extinctions to be noticed were probably the dodo *Raphus cucullatus* and Steller's sea cow *Hydrodamalis gigas* in the eighteenth century. There is now widespread recognition of the threats to species and the habitats in which they live, and most accredited zoos see the conservation of endangered species as one of their highest priorities (**Fig. 1.10**).

This chapter considers both what zoos can do, and are doing, in terms of maintaining self-sustaining populations (the *ex situ* **conservation**)

Figure 1.10 Giant waxy tree frog *Phyllomedusa bicolor*. Although this species is not yet of serious conservation concern, it is suffering increasing human pressure because its skin secretions are seen as medicinal. Amphibians as a group are under significant threat of extinction. (Photograph: Douglas Sherriff)

Figure 1.9 Captive breeding is an important function of the modern zoo, as illustrated by the successful mating of these Sumatran tigers *Panthera tigris sumatrae*. (Photograph: Jeroen Stevens)

of animals, with possible **reintroduction** to the wild for some, and their increasing involvement with *in situ* conservation. It also considers some of the problems that zoos face in deciding how many species can be maintained in zoos and which species these should be.

1.4.10 Health (Chapter 11)

A major component of the management of zoo animals is the need to ensure that they are healthy and in good condition (**Fig. 1.11**), and this is covered in **Chapter 11**.

Threats to an animal's health can often come from parasites and infections, but may also result from an inappropriate diet or some other aspect of husbandry. Inevitably, much of our knowledge of zoo animal health issues is derived from experience and case studies. This chapter reviews current practice in preventing illness and treating sick animals, and also looks at the role of veterinary staff and keepers within the zoo in relation to maintaining the good health of the animals.

1.4.11 Feeding and nutrition (Chapter 12)

Like health, the nutrition of zoo animals is an area of husbandry that relies, to a great extent, on

Figure 1.11 Maintaining health in zoo animals includes a variety of preventative measures, for example checking the oral health of animals, as in this case where a margay *Felis wiedii* is being examined. (Photograph: Colchester Zoo)

Figure 1.12 Providing a nutritionally balanced diet is only one of the considerations that have to be borne in mind when delivering an appropriate diet to zoo-housed animals, as can be seen by the variety of foods in this zoo kitchen. (Photograph: Jeroen Stevens)

experience and case studies. The natural diets of wild-living animals are often poorly known and, even if they are known, they may contain items that are difficult or impossible for the zoo to provide. Diets must be devised for zoo animals that meet their nutritional and health requirements, but also, if possible, their behavioural requirements, because foraging for and processing food are activities that often occupy a large part of an animal's time in the wild.

This chapter briefly reviews the underlying physiological and ecological theory relevant to zoo animal nutrition, and then considers how this is applied in the zoo setting (**Fig. 1.12**) to provide appropriate and nutritionally correct diets for the animals.

1.4.12 People in zoos (Chapter 13)

The zoo is a setting in which human and non-human animals[3] come into contact with one another (**Fig. 1.13**) in a very intense and intimate way, but the consequences of this had not really been studied empirically until recently. It is important to know what zoo visitors want and get from their zoo experience, and it is also important

---

[3] We know that humans are animals too, but to avoid being too wordy, we will refer to non-human animals simply as 'animals' from now on.
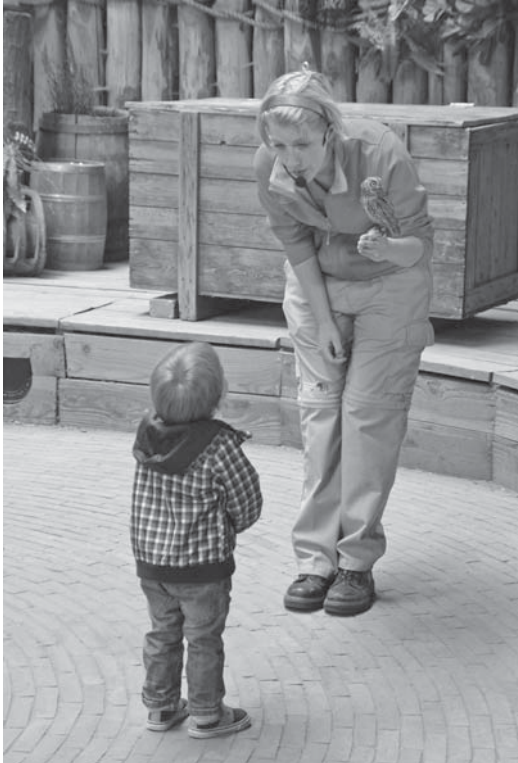
Figure 1.13 Interactions between people and zoo animals come in various forms, here as part of an educational presentation. (Photograph: Jeroen Stevens)

Figure 1.14 Good practice in the care and management of zoo animals is based on systematic scientific research. Here, a student collects behavioural data as part of an undergraduate project. (Photograph: Sheila Pankhurst)

to know if their presence and behaviour has any effect on the animals. There is also the likelihood that keepers and other zoo staff themselves play an important part in the animals' lives (**Plate 1.2**), and, in turn, affect their behaviour and welfare. These issues, together with the zoo's role in educating visitors, are considered in this chapter.

1.4.13 Research (Chapter 14)

Importantly, most of the changes that have led to the modern zoo, and the way in which zoos manage and display their animals, are built on a solid foundation of scientific research. Even as recently as the 1960s, most of what people thought they knew about zoo animals and the correct way of keeping them was anecdotal. Early attempts to record other aspects of the zoo than the basics of physical maintenance of animals were attempted

by people such as Heini Hediger, director of Zurich Zoo, but, again, his books are largely based on personal observation and experience, rather than on systematic science.

Scientific research in zoos is now a significant undertaking, encompassing areas such as behaviour (**Fig. 1.14**), nutrition, reproductive biology, and **population genetics**, among other things. This chapter examines the current state of zoo research and also considers some of the methodological issues that frequently, but usually unnecessarily, worry those about to engage in it.

1.4.14 We hope you enjoyed your visit (Chapter 15)

The final chapter of this book attempts to draw together some of the themes developed through the book, to look ahead into the future of the zoo, and to consider some of the issues that currently

Figure 1.15 The next challenge towards which zoos are working is reducing their impact on the environment, which can be achieved by moving towards sustainable operating systems in all parts of the zoo, including restaurants and shops. (Photograph: Jeroen Stevens)

confront zoos, and for which there are differing views within the zoo profession. We return again to the concept of an evidence base, and how this can be applied to all aspects of zoo operation. With current concerns about climate change and related issues such as **sustainability** now high on the political agenda (**Fig. 1.15**), we also look in this chapter to see how zoos are becoming sustainable organizations in the widest sense, with policies on sustainability affecting all aspects of the day-to-day operation of major zoos. In this chapter, we also provide information about careers in the zoo world for readers who would like to work with zoo animals or do so already.

1.5 The naming of names

Included within the text of this book are a lot of names of species of animals, of zoos, and of other organizations. Referring fully to all of them each time they are mentioned can result in a very cumbersome text and we have tried to avoid this wherever possible. It is important to identify the **scientific names** of the animals we refer to, so that we all know exactly which species we mean. We may all know what a chimpanzee is—but do we all know what we are referring to if we mention the blue poison dart frog (which you can read more about in **Box 10.3**)? Therefore we have used

the scientific name of each species when we first mention that species in each chapter, but not at subsequent mentions. (Scientific names of species are also given in the index at the end of this book.)

There is a similar problem in referring to the names of zoos. We have tried to give sufficient information for the reader to know where a zoo is when we mention it, without making a very unwieldy text. We have not used any particular rule about this—just a bit of discretion. Not all readers, for example, might know where Brookfield Zoo is, but we might expect them to know where Chicago is, so we would refer to 'Brookfield Zoo, Chicago' rather than to 'Brookfield Zoo, Chicago, IL, USA'. Where it makes it clearer, however, we have used a country name, rather than only a city name.

We have also tried not to be too cumbersome when introducing technical terms. Throughout the text, we have highlighted in bold text what we think are significant words on the first occasion that they appear in each chapter. At the end of the book is a glossary where we give brief explanations or definitions of these highlighted words. We have also included a number of footnotes in the text, which are intended as little 'asides', giving a bit more information that might illustrate or clarify a point made in the text. We hope that this, together with the index, will guide the reader through any terms that are new or unfamiliar to them.

1.6 Finally … abbreviations

We have tried very hard to make this book accessible and readable, and to avoid any unnecessary jargon. But the zoo world is riddled with acronyms and it is hard to avoid using some of these from time to time when talking about the work that zoos do. For those of you who do not know your 'EEPs' from your 'TAGs'—let alone what 'ZIMS' and 'SPARKS' might stand for—we apologize now. We have tried to explain all specialist terms and acronyms where they first arise in the text and, to make life a little easier for our readers, there is a list of acronyms at the front of the book.

Chapter 2
History and philosophy of zoos

The word zoo is now used more or less ubiquitously around the world to refer to a collection of **exotic animals** kept in captivity and on show to the general public. Yet just 200 years ago, the word 'zoo' did not exist. Before about 1800, collections of exotic animals were usually referred to as **menageries**. Many of these were private collections, kept for the amusement of wealthy individuals. It was not until after the opening of the Zoological Gardens in Regent's Park (London Zoo—**Fig. 2.1**) that the word 'zoo' came into widespread use, in the latter part of the nineteenth century.[1] Nowadays, the word 'zoo' seems to be drifting out of favour again—at least in some parts of the world—with the advent of titles such as 'safari park', 'wildlife park', and **biopark** for the wild animal collections that used to be referred to as zoos.

In this chapter, we will trace the history of zoos around the world and also look at changes in public attitudes towards wild animals in captivity (**Fig. 2.2** provides a timeline for zoos, from the menageries of ancient civilizations to the bioparks and **ecosystem zoos** of today). Zoos nowadays attract very large numbers of visitors, but can also be the subject of debate and sometimes criticism. What should be the role of zoos in today's society? Is it acceptable for zoos to keep wild animals for reasons other than conservation? Alongside an overview of zoo history, we will also briefly discuss in this chapter some of the philosophical and ethical issues that arise from keeping wild animals in captivity.

Firstly, however, a caveat: the history of zoos is a very long one, going back at least 4,000 years, and consequently a great deal of material is available about zoos throughout the ages, only a very small fraction of which can be included here. This chapter does not consider zoos in South America, for example (although there is a rich history of the keeping of exotic animals by the Aztecs and, to a lesser extent, by the Incas), nor does it look in any detail at zoos in India, Russia, or Eastern Europe. The best we can do in a book of this size is to provide suggestions for further reading at the end of each chapter, together with references to key papers and text books.

The main topics considered in this chapter are as follows:

2.1 **What is a zoo?**
2.2 **Menageries ancient and royal**
2.3 **The development of the modern zoo**
2.4 **The history of aquariums**
2.5 **Zoos today**
2.6 **The philosophy and ethics of zoos**

[1] Kisling (2001) notes that the word 'zoo' first appeared in print to describe Clifton Zoo (now better known as Bristol Zoo), but that the word was popularized as a result of a music hall song about London Zoo, 'Walking in the Zoo on Sunday'.

Figure 2.1 This illustration of the Reptile House in London Zoo in late Victorian times shows the menagerie style of exhibiting animals in closely spaced rows of cages (from John Fletcher Porter (1890) *London Pictorially Described*). (Picture: Lee Jackson, **http://www.victorianlondon.org**)

The sustainable zoo
(*zoos as environmental parks*)
21st century

The zoo as a conservation centre
Second half of 20th century

Ecosystem zoos, bioparks, and the advent of landscape immersion exhibits
1970s onwards

The 'Disinfectant Era'
1920s and 1930s (*and, in some zoos, well beyond this time*)

Hagenbeck's Tierpark at Hamburg
(*with moated, naturalistic panoramas*)
Early 20th century (*the Tierpark at Hamburg opened in 1907*)

The first American zoological gardens
Second half of the 19th century (*e.g. Philadelphia Zoo opened in 1874; the Bronx Zoo in 1899*)

The new zoological gardens of Europe
Late 18th century/early 19th century (*The Jardin des Plantes opened in 1793; London Zoo opened in 1828*)

The heyday of the royal menageries of Europe
17th century

The Tower Menagerie
The Tower Menagerie in London opened in 1245 (*and closed in 1832*)

Ancient menageries
2,000 – 2,500 BC (*e.g. in Egypt and China*)

Figure 2.2 This figure shows some of the major developments in the history of zoos throughout the ages. The timeline is not drawn to scale. (Diagram: Sheila Pankhurst)

Special topics, such as zoo architecture and the **ethics** of keeping animals in captivity, are included in boxes throughout this chapter, as are brief accounts of some iconic individual zoo animals, the stories of which mirror a particular period in zoo history. These animals include Jumbo, an African elephant *Loxodonta africana* at London Zoo, and Willie B., a western lowland gorilla *Gorilla gorilla gorilla* housed at what is now Zoo Atlanta in Georgia, USA. There are also short accounts of influential curators and zoo directors, such as Abraham Dee Bartlett, William Conway, Gerald Durrell, and David Hancocks.

2.1 What is a zoo?

In **Chapter 1** of this book, we looked at how zoos are defined and also set out the scope of this book, which is largely concerned with **accredited zoos**. Therefore the focus of this book broadly reflects the definition of a zoo provided by Norton *et al.* in *Ethics on the Ark* (1995), which opts for the definition of a zoo or aquarium as:

> 'A professionally managed zoological institution accredited by the American Zoo and Aquarium Association and having a collection of living animals used for conservation, scientific studies, public education, and public display'.

(We might, perhaps, add a sentence or two about due regard for animal welfare, and delete the word 'American'.)

In contrast, Baratay and Hardouin-Fugier, in their book *Zoo: A History of Zoological Gardens in the West* (2004), offer a harsher definition of a zoo as '*a place of forced meeting between animal and human*'. But note that this definition could also be used to describe farms, some laboratories, and, indeed, even many ecotourism sites.

What a zoo is—and what a good zoo should be—may, of course, be two very different things. Most readers of this book would probably tend towards the Norton *et al.* (1995) definition as a description of what a good zoo should be, but will, at the same time, be aware that there are

many zoos in the USA, Australia, Europe, and the rest of the world that fall far short of these standards.

The US Association of Zoos and Aquariums (AZA)[2] , on its website (**http://www.aza.org**) describes its members as follows:

> 'AZA-Accredited Institutions represent zoological parks or aquariums that maintain both a professional staff and a more-than-token collection of wildlife, providing the collection with appropriate care, exhibiting them in an aesthetic manner on a regularly scheduled, predictable basis. Institutional Members have as their primary business the exhibition, conservation, and preservation of the earth's fauna in an educational and scientific manner'.

It is a definition that, interestingly, acknowledges explicitly that there is, or should be, an aesthetic component to zoos.

2.2 Menageries ancient and royal

Although the zoo in the form which we are now familiar with is a relatively recent phenomenon, the keeping of exotic animals in menageries has a long history and there is evidence of these kinds of collection from the ancient world dating back at least 4,000 years.

---

[2] AZA is the USA's leading accrediting organization for zoos and aquariums, and has its offices in Maryland, just outside Washington, DC. There is no 'A' for American in the acronym.

2.2.1 The ancient menageries

In Egypt, the earliest known records of exotic animals kept in captivity go back to around 2,500 BC. Pictures and hieroglyphics at Saqqara cemetery, near Memphis, show that the Egyptians kept many species of antelope in captivity, as well as baboons,[3] hyaenas, cheetahs, cranes, storks, and falcons (Lauer 1976). Other records from ancient Egypt show that Tutmosis (Thutmose) III kept wild animals in the gardens of the famous temple at Karnak, near Luxor (Strouhal 1992), and the Pharaoh Rameses II, who reigned over Egypt from 1298 to 1235 BC, kept giraffes, as well as a pet lion that accompanied him into battle (Kisling 2001).

In Mesopotamia (the area between the Tigris and Euphrates rivers, largely within the borders of modern-day Iraq), there are records of lions being kept in captivity by royalty earlier than 2,000 BC. Carvings of other wild animals, including monkeys, elephants, and antelopes, appear on the walls of Assyrian royal palaces (Kisling 2001). The earliest **ecosystem exhibit** may even date back to ancient Mesopotamia. Records show that Sennacherib, king of Assyria from 704 to 681 BC and believed to be the creator of the famed Hanging Gardens of Babylon, also created an artificial wetlands environment in order to exhibit marsh plants and animals (Dalley 1993). (Further information about ecosystem exhibits is provided in **section 2.3.5** and **Box 2.6**.)

During the Zhou dynasty (c. 1000–200 BC) in China, walled-in parks were created to house animals. The later Han dynasty (from c. 200 BC) saw the creation of private menageries comprising animals such as birds, bears, and tigers; one of the large royal parks of the Han period contained animals such as alligators, deer, elephants, and rhinoceroses (Schafer 1968).

The ancient Greeks kept collections of wild animals for study and enlightenment, as well as for show. Aristotle (384–322 BC), for example, had his own private menagerie and wrote the earliest known zoological encyclopedia, *The History of Animals*, in 350 BC.

2.2.2 The Roman gladiatorial menageries

The Romans kept many wild animals—not so much for education and contemplation, but rather for slaughter in the gladiatorial arena, often on a grand scale. Any visitor to Rome today can still see clearly at the Colosseum the extensive subterranean holding areas for men and exotic animals. Archaeological evidence points to the use of sophisticated winches and elevators or lifts to bring large animals up from their pens below ground to the level of the arena (**Fig. 2.3**).

Baratay and Hardouin-Fugier (2004) suggest that the Roman practice of killing large wild animals for public entertainment developed from the symbolic slaughter of animals such as elephants captured from their enemies in battle '*to avenge the losses inflicted by military* **pachyderms**'. Whatever the antecedents for this public killing, the scale of the slaughter in arenas such as the Colosseum was immense (Jennison 2005). The Roman general Pompey, for example, is reported to have financed a single show in which twenty elephants, 500 or 600 lions, and numerous other animals were killed (Kyle 2001). The logistics of capturing, transporting, and maintaining in captivity 500 or 600 lions are astounding and beg the question of how many more lions died before reaching the Colosseum.

The slaughter of so many animals (and humans)[4] for public entertainment meant that many wild beasts became rare, or even locally

---

[3] **Scientific names** of species have only been provided in this chapter where there is reasonable certainty over the identity of the species being referred to. Many historical accounts of early menageries and zoos refer to animals such as 'tigers' or 'the elephant', without giving further details.

[4] It is unthinkable nowadays that large numbers of human lives could be viewed as being readily expendable in the cause of public entertainment. This serves to highlight the very different attitudes to non-human animals that have prevailed at different times throughout history (and that still prevail, to some extent, in different cultures today).
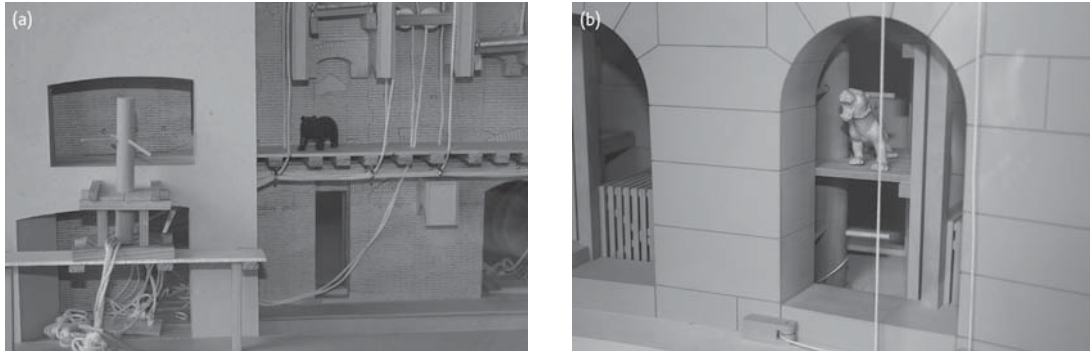
Figure 2.3 These models show the complex system of lifts and pulleys that was employed to raise animals from underground storage areas up to the arena in the Colosseum, in ancient Rome. (Photographs: Geoff Hosey)

extinct, in Roman times. The Roman appetite for contests between man and beast is believed to have contributed to the extinction of the hippopotamus from Nubia, the lion from Mesopotamia, the tiger from modern-day Iran, and the elephant from northern Africa (today, the African elephant is a sub-Saharan animal).

2.2.3 From the Dark Ages to the royal menageries of Europe of the seventeenth century

There are very few records of zoos of any kind during the Dark Ages and medieval times (from the fall of the Roman Empire in the fifth century to around AD 1450). Exceptions are the collections of exotic animals maintained during this time at Baghdad, Cairo, and Istanbul (Constantinople), and also in the parks and gardens of the Yuan and Ming dynasties in China (Kisling 2001). In Western Europe, Kisling (2001) records that the Emperor Charlemagne (AD 742–814) maintained animal collections at several of his royal estates, with animals such as elephants, lions, bears, and camels among the inhabitants. In Britain, Henry I (the son of William the Conqueror) enlarged an animal collection that had been started at Woodstock in Oxfordshire by his father; this menagerie included lions, leopards, lynx, and camels.

In the thirteenth century, the Holy Roman Emperor Frederick II was the first person in several hundred years to establish a major new zoo in Europe. This was at Palermo in Italy, and the collection included elephants, a giraffe, leopards, camels, and monkeys. Frederick II wrote several authoritative books on birds and falconry, and set up permanent zoos in three other Italian cities. He also contributed to the history of zoos elsewhere in Europe as a result of his habit of sending wild animals as gifts to other European heads of state—notably, to his brother-in-law, England's Henry III. Three leopards sent from Italy to Henry III became the first inmates of the infamous royal menagerie in the Tower of London; these animals were later represented on Henry III's coat of arms (Keeling 1984).

During its heyday in the seventeenth century, the animal collection at the Tower of London was typical of the zoos of its time: a private collection of exotic animals kept initially for the entertainment of the king and his court. By the late sixteenth century, nearly all kings and princes in Europe had at least one private menagerie. These collections were rarely open to the public; they were emblems of state, and the animal houses were often elaborate and lavish. The Dutch were a notable exception, building zoos as places of study which were open to the public for a fee.

This era of zoos in Europe existing largely as private royal collections lasted for around 200 years, extending well into the eighteenth century. One of the most stylish of the royal zoos of

the seventeenth century was that of Louis XIV at Versailles, with its formal symmetrical ground plan, and elaborate sculptures and decoration. Unfortunately, the fate of many of the animals in the Versailles menagerie was slaughter by the proletariat during the early days of the French Revolution. (A few of the Versailles animals did survive and were later transferred to the Jardin des Plantes in Paris, of which more in the next section.)

At the same time—and in stark contrast to the gardens at Versailles, which were accessible only to a small elite—travelling circuses and exhibitions put on by showmen moving from town to town meant that ordinary people could still see exotic animals. From the sixteenth to the eighteenth centuries, there are numerous records of wild animals, including elephants, tigers, and bears, being transported in wagons to the towns and villages of Europe (Baratay and Hardouin-Fugier 2004).

2.3 The development of the modern zoo

From the start of the eighteenth century onwards in Europe, zoos saw a change not so much in the animals they kept, or how they kept them, but in their audiences. Gradually, through the eighteenth and nineteenth centuries, zoos became public places, rather than private and exclusive menageries usually reserved for royalty or the very rich and powerful. This change in zoo audiences mirrored a wider public interest in natural history, as exploration and the growth of the various European empires saw more and more exotic animals brought back from travels in far-flung corners of the world. By the nineteenth century, the 'modern' zoological garden had been born, with the Jardin des Plantes in Paris

and Regent's Park Zoo in London vying for position as world leaders.

2.3.1 The new zoological gardens of Europe of the eighteenth and nineteenth centuries

The nineteenth century is regarded by many as a golden age of exploration and natural history. Specimens brought back from expeditions (not least Charles Darwin's voyages on *The Beagle*) led to a rapid growth in the size and importance of natural history museums and, by association, zoological and botanical parks and gardens.

The Jardin des Plantes, Paris

In Paris, a new public menagerie was created in 1793, on the site of the old Jardin du Roi (renamed during the French Revolution as the Jardin des Plantes). This operated as a division of the Muséum d'Histoire Naturelle (Museum of Natural History), for which two new chairs of zoology[5] were established. There is some evidence that the academics and administrators of the Paris Museum of Natural History had not intended to create a menagerie; the new name of the site was, after all, the Jardin des Plantes. Ownership of a number of wild animals was forced upon the Museum when the police department took action to confiscate exotic animals from the many travelling exhibitors in and around Paris, and delivered these to the Museum (**Fig. 2.4**). The first scientific director of the Jardin des Plantes was Étienne Geoffroy Saint-Hilaire; his colleague and another distinguished professor at the Museum of Natural History was Georges Cuvier, known for his detailed paintings of plants and animals (Kisling 2001).

However, it was Frédéric Cuvier (**Fig. 2.5**), Georges' younger brother, to whom the day-to-day responsibility of managing the animals in the new menagerie was given, from 1804 onwards.

---

[5] One of the new chairs of zoology at the Museum of Natural History in Paris, the wonderfully named 'Chair of Insects and Worms', went to Jean-Baptiste Lamarck, now better known for his controversial theories of evolution.
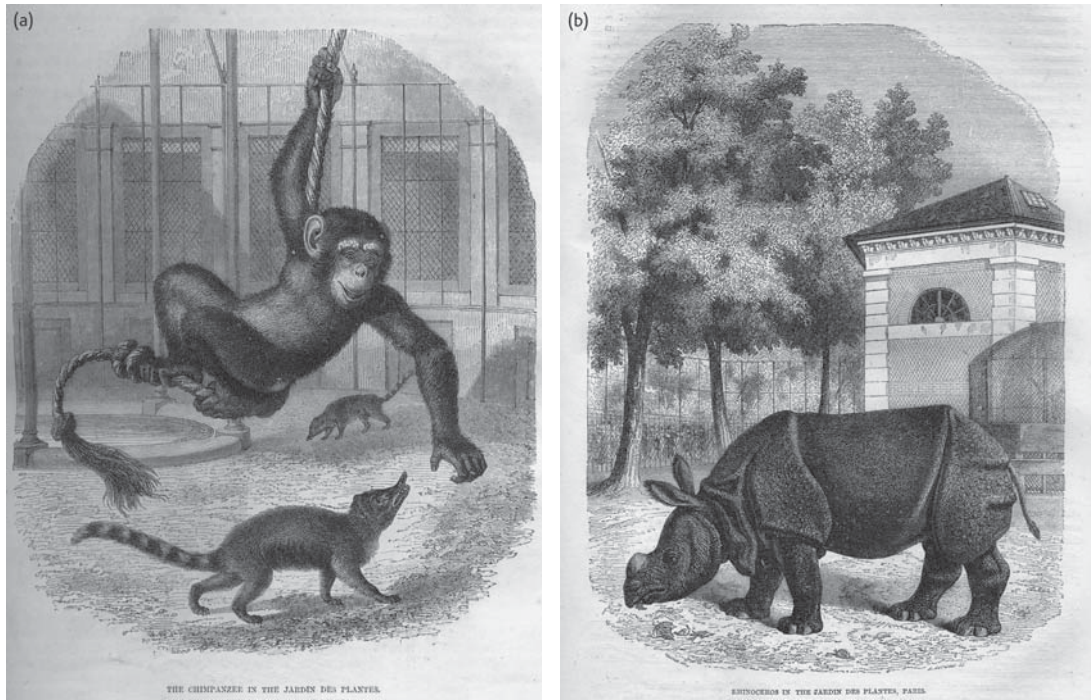
Figure 2.4 These drawings of (a) a chimpanzee *Pan* spp. and (b) an Asiatic rhinoceros *Rhinoceros unicornis* at the Jardin des Plantes around about the middle of the nineteenth century show that the manner of keeping animals in Paris at that time was not unlike that which we saw in London in **Fig. 2.1**. (Pictures from *Cassell's Popular Natural History*, not dated)

Figure 2.5 Frédéric Cuvier was probably the first ever curator of a national zoo and he held that post for more than 30 years at the beginning of the nineteenth century, during which time he ensured that the Jardin des Plantes became a focus of scientific study. (Picture from *Cassell's Popular Natural History*, not dated)

Cuvier's post, which he held for more than 30 years (to 1838), was one that had never really existed before—curator or scientific superintendent of a national zoo that was open to the public (Burkhardt 2001). Consequently, the young Cuvier had to learn quickly how to care for the exotic animals arriving at the Jardin des Plantes from all corners of the world. As he wrote, rather despondently, in his first guidebook to the zoo: '*Nothing has been written, nearly nothing has been seen, everything remains to be done.*'

Cuvier's background was as a chemist, and his belief that menageries could become for zoologists what laboratories were for chemists helped to lead to the rapid establishment of the Jardin des Plantes as a place for scientific study, with the live animals in the menagerie as much a focus of research as the dead specimens in the adjacent museum (Burkhardt 2001). Cuvier was an early pioneer of the study of animal behaviour and demonstrated a keen interest in what we would

Figure 2.6 This cage, in which zoo visitors are currently standing, is one of the old animal enclosures at Vienna Zoo. The cheetahs *Acinonyx jubatus,* which could formerly have been housed inside a cage like this, are now in a large enclosure outside and the cage has been appropriated for visitor use. (Photograph: Vienna Zoo)

now refer to as animal welfare and **enrichment**. Of the raccoons in his care, for example, he wrote:

> 'It would be necessary to see them under other conditions, that is to say sufficiently free and under circumstances sufficiently diverse, so their faculties could be in some measure developed.'
>
> (Burkhardt 2001)

Tiergarten Schönbrunn (Vienna Zoo)

Another notable European zoo founded in the eighteenth century (and one that is still going strong today, under the proud title of 'Europe's oldest zoo') is the Tiergarten Schönbrunn in Vienna (**Fig. 2.6**), founded in 1752[6] by the Emperor Franz Stephan. Collections of exotic animals at Schönbrunn are recorded well before the eighteenth century, but these were private affairs (the menageries

---

[6] Some sources give 1751.

of royalty and noblemen), whereas Vienna Zoo was open to the public from the start and, indeed, entrance to the Tiergarten at Schönbrunn was free of charge from its creation until 1918.

Animals for the Vienna Zoo arrived only gradually, bought from the travelling menageries of the time or captured by Emperor Josef II's expeditions to Africa and the Americas. The first elephant to be exhibited at Schönbrunn arrived in 1770, marking the start of a long tradition of elephant keeping at Vienna that resulted, in 1906, in the first birth of an elephant in captivity in Europe, and, in 2001, in the birth of the first test-tube baby elephant, named Abu.

Regent's Park Zoo, London

What is now London Zoo, in Regent's Park, was the brainchild of Sir Stamford Raffles (who also founded the port of Singapore). Prompted by the growing reputation of the Jardin des Plantes

Box 2.1   JUMBO THE ELEPHANT

David Hancocks opens the first chapter of his book *A Different Nature: The Paradoxical World of Zoos and their Uncertain Future* (2001) with an account of the first elephant to be housed at London Zoo. This was a young male African elephant named Jumbo. Captured from the wild in Ethiopia and subsequently purchased by an animal dealer, Jumbo arrived at London Zoo in 1865. He grew up to be a magnificent specimen, fed on a daily diet that reportedly included bread, biscuits, and cakes, as well as hay and oats (Preston 1983). Members of the public could, for a small payment, ride on Jumbo, and he was well known and much loved by London Zoo's visitors.

After 17 years in captivity, however, Jumbo started to show periodic outbursts of aggressive behaviour when he became difficult to handle. When, in 1882, the Zoo was offered a large sum of money for Jumbo by Phineas T. Barnum, of Barnum and Bailey's Circus in the USA, the Council of the Zoological Society of London gratefully accepted, relieved to have been given an opportunity to get rid of an animal that the Zoo was no longer confident it could control. The news that Jumbo was to be sold—and worse, sold to a circus in the USA—generated a huge public outcry (Barrington-Johnson 2005; **Fig. 2.7**), but the Council stood by its decision and Jumbo was transported to the USA. The massive elephant was a star of Barnum and Bailey's Circus for three years, before being killed in a freak collision with a freight train.

Even before his untimely death, Jumbo had become something of an icon. His name came into popular use to denote anything of a grand size (Barrington-Johnson 2005), from cigars to jars of peanut butter. Passengers travelling on jumbo jets today probably do not realize that the popular name for these planes has its origins in the name of a zoo elephant. As David Hancocks (2001) points out: '*No other animal's name has become so deeply embedded in our language*'. Jumbo's story, as Hancocks reminds us, is of an animal captured from the wild as an infant, sold on to a dealer and then to a zoo, fed an inappropriate diet, displayed as a curiosity in an unnatural setting, used as a plaything for visitors to ride upon, and finally meeting an untimely death. Hancocks ends his account of Jumbo's life by saying: '*Jumbo's display brought out the best and worst in people. Like many other zoo animals, and like many zoos themselves, Jumbo satisfied the curiosity of all, the vanity of many and the greed of a few*'.

There is a postscript to Jumbo's story. The skeleton of this massive animal ended up at the American Museum of Natural History, in New York. More than a century after the elephant started to behave unpredictably and dangerously, the curator of mammals at the museum, Richard Van Gelder, noticed that the molars in Jumbo's jaw were growing inwards rather than erupting properly (Van Gelder 1991). This abnormal pattern of tooth development was no doubt due, at least in part, to the unsuitable low-roughage diet Jumbo had been fed in captivity. The probable pain from these impacted molars provides a highly plausible explanation for the animal's increasingly aggressive and erratic behaviour.
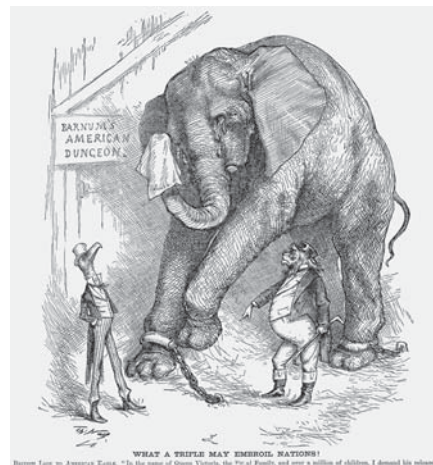
Figure 2.7 When Jumbo was sold by London Zoo to Barnum and Bailey's Circus in the USA, the resulting public outcry was encapsulated in the British press in cartoons such as this one. (Picture: **http://www.historypicks.com**)

in Paris as a centre for scholarly activity, Raffles drew up a prospectus for a new academic society and zoo in London. The Zoological Society of London's first council meeting was held in May 1826; the zoo in Regent's Park opened just under two years later, in 1828.

The Zoological Gardens were an instant success with the public (**Fig. 1.2**) and became a fashionable place to be seen (Hancocks 2001). A song, 'Walking in the Zoo on Sunday', by a music hall artist called the Great Vance, became a hit and the word 'zoo' gradually entered popular vocabulary (Bostock 1993). Sadly, Raffles did not live to see his vision materialize; he died of a stroke, in July 1826, on his 45th birthday (Barrington-Johnson 2005).

During the second half of the nineteenth century, London Zoo developed many innovative exhibits (**Fig. 2.8**), including the first reptile house in the world (in 1849); this was followed by the first public aquarium, in 1853, and the first insect house, in 1881 (Hancocks 2001; see **Box 2.1**). The first children's zoo opened in 1938. The Zoo was also remarkably successful at keeping and breeding wild animals in captivity at this time.[7] Its records for the period between 1860 and 1880 show that species bred in the Zoo included the giraffe, the spotted hyaena *Crocuta crocuta*, the chevrotain *Hyemoschus aquaticus*, a species of giant skink, the sunbittern *Eurypyga helias*, and many others (Kisling 2001).

For a time, London Zoo was a world leader and spawned many imitations around the world. Not until 1907, with the opening of Carl Hagenbeck's zoo in Hamburg, did the pattern of zoo development take another great leap forward.

London Zoo's influence was due to two key factors:

- firstly, it was founded on scientific principles (more on these in a moment);
- secondly, it was created in a large public open park with informal naturalistic landscaping.

Figure 2.8 This is a view of the lion house at London Zoo in 1896. The building was sizeable (234 ft × 50 ft), and was warmed and ventilated. The cages, which were seen as large in their day, were separated from the public by a broad barrier. This was seen as an advanced design for animal exhibitory in Victorian times. (Photograph: Lee Jackson, **http://www.victorianlondon.org**)

The prospectus for the Zoological Society of London (ZSL), under whose auspices London Zoo was created, stated that the Society would acquire '*animals … from every part of the globe … as objects of scientific research, not of vulgar admiration*' (Olney 1980). Another objective of the ZSL was '*the advancement of zoology and animal physiology*'. Initially, the zoo in Regent's Park developed along **taxonomic** lines, with collections based on representative members of a single genus.

2.3.2 Hagenbeck and the Hamburg Tierpark

After the Jardin des Plantes and London Zoo, the next great leap forward in zoo design was prompted not by a scientist or an architect, but by a German animal dealer and trainer, Carl Hagenbeck. Although Hagenbeck is best remembered now for the design of naturalistic zoo enclosures, in his day he was also known as a prolific animal collector and trader, counting

---

[7] The captive breeding of native species in zoos is not only a recent development. London Zoo was successfully breeding British adders *Vipera berus*, grass snakes *Natrix natrix*, and smooth snakes *Coronella austriaca* in the 1850s, soon after the opening of the new reptile house (Kisling 2001).

Barnum and Bailey's Circus among his many customers (Rothfels 2002).

Hagenbeck's vision was of a zoo without bars, based on images of natural habitats (**Fig. 2.9**). He began with a series of travelling displays, which he referred to as 'panoramas', and then—in collaboration with Urs Eggenschwyler, a Swiss sculptor—he developed a permanent zoo park with concrete and cement rocks and gorges, based on real geological formations (Hancocks 2001). This was the Tierpark at Stellingen near Hamburg, which opened in 1907 and was, from the outset, a huge success with the German public. Visitors flocked to see the artificial mountain landscape built to house African animals and the 'Polar Panorama' with its Arctic animals (Rothfels 2002).

Hagenbeck's panoramas marked the beginning of a move away from collections presented on taxonomic lines towards collections representing the fauna of regions of the world, such as the African savannah or the Arctic. But perhaps the greatest legacy of Hagenbeck and Eggenschwyler is their use of moats and ditches, rather than fences and bars, to separate animals from visitors. In this respect, they took zoos 'beyond the bars' at the start of the twentieth century. Hagenbeck, who was an accomplished animal handler and trainer as well as a dealer, carefully calculated the maximum distance that animals such as lions and tigers could jump before building his moats. He later wrote of the animals in his zoo:

'I wished to exhibit them not as captives, confined within narrow spaces and looked at between bars, but as free to wander from place to place within as large limits as possible'.

(Hagenbeck 1909)

Figure 2.9 This old photograph shows one of the panoramas designed by Carl Hagenbeck for the Hamburg Tierpark. Hagenbeck pioneered the use of moats, rather than cages and bars, to separate animals from zoo visitors. (Photograph: courtesy of the Archiv Hagenbeck, Hamburg)

Box 2.2 THE LAST PASSENGER PIGEON

Cincinnati Zoo in Ohio was the home of the last known passenger pigeons *Ectopistes migratorius.* These birds were once found in vast numbers across the eastern USA and Canada, but, by the early part of the twentieth century,
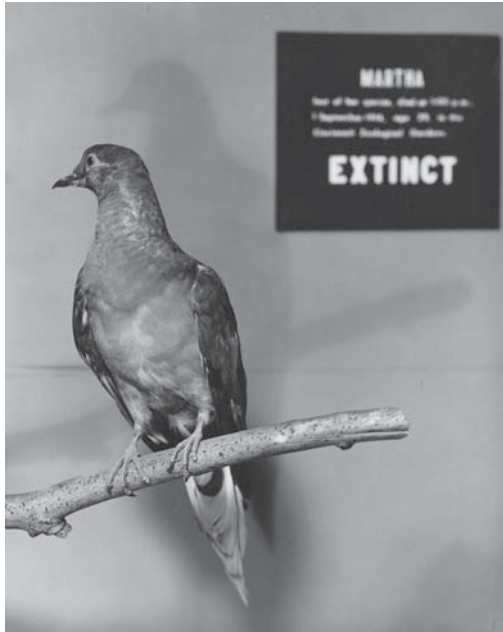
the species had become extinct. The loss of the passenger pigeon is made all the more dramatic by the historical reports of the size of the flocks of this bird, which probably numbered in the hundreds of millions. Schorger (1955) has estimated that, in the time of the naturalist John James Audubon (1785–1851), one in every four birds in North America was a passenger pigeon. Early settlers reported flocks taking several hours to pass overhead and told of the sky being darkened by the multitude of birds (Kisling 2001).

Despite some initial success at breeding passenger pigeons, Cincinnati Zoo's small flock dwindled from twenty individuals in 1881 to just three surviving birds by 1907. A female known as Martha, the last of these birds, died in 1914 and, with her death, the species vanished (Schorger 1973). Martha's body was presented to the Smithsonian Institution in Washington (**Fig. 2.10**), and Cincinnati Zoo has preserved the aviary in which she lived as a memorial to all endangered species (Kisling 2001).

Figure 2.10 This photograph shows the stuffed body of Martha, the last surviving passenger pigeon *Ectopistes migratorius*. After Martha died in 1914 at Cincinnati Zoo, her body was presented to the Smithsonian Institution in Washington. (Photograph: Smithsonian Institution Archives)

2.3.3 The first zoological gardens in America

Prompted by developments in Europe, the USA saw the creation of its first zoological parks towards the end of the nineteenth century. Philadelphia Zoo, in Pennsylvania, opened in 1874 with its mission to educate and entertain, and Cincinnati Zoo, in the state of Ohio, opened in 1875 (see **Box 2.2** for the story of a species extinction that happened at this zoo); other cities soon followed. The New York Zoological Park, better known as the Bronx Zoo,[8] opened in 1899.

By comparison with Europe, the history of North American zoos only stretches back to a little over a century ago. The USA had circuses prior to the nineteenth century, and there were travelling menageries and some private collections of exotic animals, but there were none of the elite menageries associated with wealth, power, and royalty that were typical of European countries. The new North American zoos were civic institutions (**Fig. 2.11**), and unlike the major 'new' zoos in Europe, did not (usually) develop out of links to museums or universities (Hanson 2002). A number of the early zoological gardens in the USA were quick to follow Hagenbeck's lead and built naturalistic moated enclosures; these zoos included those

---

[8] The parent body of the Bronx Zoo in New York is the Wildlife Conservation Society (WCS).

Figure 2.11 An early picture from an American zoo, showing schoolchildren feeding bears at the Smithsonian's National Zoo in 1899 (Photograph: Smithsonian's National Zoo)

of Denver, St Louis, Chicago, and Cincinnati (Kisling 2001).

2.3.4 The 'Disinfectant Era'

The 1920s and 1930s saw the start, in some zoos, of a depressing move away from Hagenbeck-inspired naturalistic exhibits towards 'modern' and often minimalist enclosures. In the interests of hygiene, cages were designed primarily for ease of cleaning rather than with regard to the needs of the animals housed within them (Hancocks 2001).[9] The trend for sterile cages with concrete floors and tiled walls persisted well into the 1960s and 1970s. Regrettably, cages of this type can still be seen in many European zoos (**Fig. 2.12**). This period of zoo design and management is

sometimes referred to as the **Disinfectant Era** (Hancocks 2001) or the **Hygiene Era**. As Hancocks (2001) has pointed out, the use of tiled walls, concrete floors, plate-glass viewing windows, and steel doors in many of these minimalist en-closures leads to an environment that is not only sterile, but which is likely to be noisy in a way that promotes increased stress, with the sound of steel doors '*reverberating at a painful level in the hard acoustics of the cages*' (see **Box 2.3**).

Architects such as Russian-born Berthold Lubetkin (principal partner in the Tecton Group) must take their share of the blame for the sterile minimalist designs adopted in many zoos in the 1930s. For a period of time, form came before function and the animals' needs often came a very poor second to architectural impact.

---

[9] Both Heini Hediger (known as 'the father of zoo biology') and William Conway have referred to architects as the most dangerous animals in the zoo.

Figure 2.12 This tiled enclosure, with its smooth shiny floor, is a good example of an enclosure that has been built with hygiene as its priority, because its design facilitates easy cleaning. When captive animal management was still in its infancy, it was thought that preventive health care and the elimination of disease risk would ensure healthy and reproductively active animals. (Photograph: Sheila Pankhurst)

Lubetkin's penguin pool at London Zoo is perhaps the best-known example of a zoo building or enclosure from this period. Completed in 1934 with the assistance of Danish structural engineer Ove Arup and highly regarded by other architects, the pool is now a Grade I listed structure (see **Box 2.4** for further information about zoo architecture and listed buildings). But it was never a particularly successful home for the penguins, and the birds were eventually moved out in 2004 to a more naturalistic pool, and then in 2011 to a new £2million 'Penguin Beach' exhibit, with England's largest penguin pool.

It is worth pointing out, however, that public reaction against some of the worst enclosures of the Disinfectant Era may well have speeded up the advent of the modern zoo, with its naturalistic settings and a new emphasis on seeing animals within the context of their ecosystem.

2.3.5 The advent of ecosystem exhibits, bioparks, wildlife parks, and safari parks

The impetus for change

For a number of US and European zoos, the 1950s 1960s, and 1970s were a period of stagnation and, in many cases, decline. The beginnings of an environmental movement in the 1960s, and of an **animal rights** movement in the 1970s, saw increasing public concern about poor zoos and even about whether zoos should exist at all (Donahue and Trump 2006; see **section 2.6.2** on anti-zoo campaigns). The growth in television programmes about wildlife emphasized the contrast between animals in sterile, badly designed enclosures, and the same species roaming free in their natural habitat. At the same time, people were being offered greater choice in how they spent their

Box 2.3   WILLIE B., THE STORY OF A LOWLAND GORILLA

'*On a rainy day in May 1988, a lowland gorilla named Willie B. stepped outdoors for the first time in twenty-seven years*'. Elizabeth Hanson (2002) begins her excellent book about the history of American zoos with an evocative account of the story of an individual animal, a male western lowland gorilla *Gorilla gorilla gorilla* captured from the wild in Africa and acquired in 1961 by the zoo in Atlanta, Georgia. This was Willie B., who was housed, by himself, in an indoor enclosure with a concrete floor. Photographs from that time show an overweight animal, surrounded by bars and tiled walls (**Fig. 2.13a**).

Twenty-seven years later, in 1988, a new naturalistic gorilla exhibit was created at the Zoo, now renovated and renamed Zoo Atlanta. For the first time at the Zoo, Willie B. was able to step outside onto grass, amid trees (**Fig. 2.13b**). Willie B. lived on at Zoo Atlanta for another 12 years, during which time other gorillas were introduced into the exhibit. Willie B. even became a successful father, siring five surviving offspring (his second, a female gorilla born in 1996, was named Olympia to commemorate the Atlanta Olympics). He died in 2000, at the age of 41; more than 7,000 people attended a memorial ceremony held by the Zoo, and today visitors to Zoo Atlanta can see a large sculpture of Willie B. in a special garden near the gorilla enclosure. As Hanson puts it: '*In his lifetime he had journeyed from being an object of voyeurism in a sterile cage to a muscular silverback, foraging for raisins and behaving like a gorilla.*'

The story of Willie B. encapsulates both the depressing era of hygienic, but sterile, zoo cages, with their easy-to-clean tiled walls and concrete floors, and also the advent of the new biopark zoo, with naturalistic exhibits designed to encourage animals to behave as they would in their natural habitat. Hanson points out that, during Willie B.'s lifetime, zoos in the USA, Europe, and elsewhere moved from collecting animals from the wild to participating in **captive management programmes**. Visitors to zoos no longer expected to see animals behind bars; zoos, in turn, began to take on more of a role in promoting the conservation of species such as gorillas.

Figure 2.13 Willie B., a lowland gorilla *Gorilla gorilla*, was one of the best-known and best-loved residents of what is now Zoo Atlanta, in Georgia. The two photographs here show him (a) housed alone in a tiled indoor enclosure and (b) after he was moved into a new naturalistic outdoor enclosure. Other gorillas were gradually introduced into the new outdoor exhibit and Willie B. went on to father five offspring. (Photographs: courtesy of Zoo Atlanta)

Box 2.4 ZOO ARCHITECTURE AND PROTECTED BUILDINGS

Older city centre zoos, in particular, often have to manage their animals within constraints imposed by old and unsuitable buildings. This job is made more difficult when these buildings have some kind of legal protection, so that they cannot be demolished or even substantially altered without special permission. Within the UK, for example, a 'listed building' refers to a building included in the national List of Buildings of Special Architectural or Historic Interest. Buildings on this list are graded into categories according to their architectural or historical importance (Grades I and II* are the top categories) and are subject to additional planning controls and protection. Listed building consent is required not only to demolish a listed building or any part of it, but also to alter the building in any way that would affect its character, internally or externally.

London Zoo faces a special challenge in this respect (it has a rich architectural heritage, particularly if you happen to like early concrete structures). As well as Lubetkin's famous penguin pool (**Figs 2.14a** and **2.14b**), London Zoo has nine other Grade I or Grade II listed buildings, and even the smallest alteration to the fabric of these buildings requires special permission. These buildings include Hugh Casson's concrete elephant house, built in the early 1960s, and the 1932 gorilla house or 'Round House', another Lubetkin building (Barrington-Johnson 2005). (Further information about London Zoo's architectural heritage can be found online at **http://www.zsl.org/info/about-us**—there is a link to ZSL architecture.)

The constraints imposed by the listed status of these buildings at London Zoo have invariably resulted in the animals that they were originally designed to house being moved elsewhere, to new sites or enclosures in which modern standards of welfare and husbandry can more easily be provided (the elephants have gone to Whipsnade Wild Animal Park near Dunstable; the gorillas are
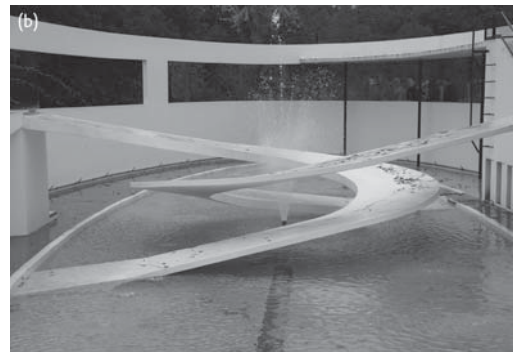
Figure 2.14 (a) and (b) The old penguin pool at London Zoo is a Grade I listed building, designed by Russian-born architect Berthold Lubetkin in the 1930s. (c) Another early concrete structure designed by Lubetkin's Tecton Group of architects, this time at Dudley Zoo, where it was used for many years to house polar bears, as shown in this photograph taken in 1960. More recently, it has been accepted that enclosures like this do not meet the needs of the animals for which they were designed. However, many such enclosures are now listed buildings and therefore cannot be demolished. (Photographs: (a) and (b) Chris Sampson/CC-BY; (c) Geoff Hosey).

still at London, but are now housed in the £5.3m Gorilla Kingdom exhibit, which opened in March 2007). This leaves the Zoo with buildings it almost certainly will not be allowed to demolish, or even substantially alter, but which are unsuitable for housing many of the species that the Zoo would like to keep.

Other zoos face similar problems: Bristol Zoo's former Giraffe House, as well the main entrance lodge and the south gates, are Grade II listed buildings; Dudley Zoo, in the West Midlands, has no fewer than twelve Lubetkin and Tecton listed buildings (**Fig. 2.14c**), of which five are categorized as Grade II*.

leisure time (Kisling 2001). To survive, zoos had to compete with a range of other recreation facilities, from theme parks or amusement parks to better and more accessible sports facilities.

In the face of increasing criticism and declining visitor numbers, zoos in the latter half of the twentieth century needed to reinvent themselves,

or face an uncertain future and the possibility of closure. Some zoos did close; others rose to the challenge of reinvention and emerged from a process of radical, and sometimes painful, change as a new generation of ecosystem zoos, wildlife parks, and bioparks. (**Box 2.5** looks at pioneering zoo directors, such as William Conway at the

Box 2.5 PIONEERING ZOO DIRECTORS AND CURATORS

One of the best-known directors of London Zoo in Victorian times was Abraham Bartlett, who was appointed as Superintendent of the London Zoological Gardens in 1859 (the same year, incidentally, that Darwin published *On the Origin of Species*). He was then paid the princely salary of £200 p.a. (Blunt 1976). Bartlett held the post of Superintendent for 38 years, until his death in 1897 (Vevers 1976). During this time, he had to take responsibility for species sent to the Zoo from all over the world, many of which had never been kept in captivity before, and for which he had to develop appropriate diets and housing.

Bartlett proved to be a resourceful and highly successful director of the Zoo (Barrington-Johnson 2005) and many 'firsts' in the captive breeding of exotic animals were recorded at London Zoo during his tenure. He also kept extensive and detailed notes of the animals in his care, and of their husbandry, which were used as the basis for the posthumous publication of two books, *Life Among Wild Beasts in the Zoo* (1890) and *Wild Animals in Captivity* (1898).

Almost a century later, in 1956, a young curator from St Louis[10] Zoo in Missouri, named William Conway, joined the Bronx Zoo as its Associate Curator of Birds (Hancocks 2001). By 1962, Conway was the Zoo's Director, and by 1966, he was General Director of the New York Zoological Society—which became the Wildlife Conservation Society (WCS) in 1993. He eventually became President of WCS as well, a post that he held until his retirement in 1999 (**Fig. 2.15**).

Together with other 'zoo pioneers' such as Gerald Durrell at Jersey Zoo and George Rabb at Brookfield Zoo in Chicago, Conway was at the forefront of moves to make conservation a central role of zoos. He was also largely responsible for putting the Bronx Zoo on the world map as a leading example of what zoos could and should be doing, developing innovative and naturalistic exhibits such as The World of Darkness and The World of Birds. But perhaps Conway's greatest contribution to setting the standards for modern zoos was his emphasis on the Zoo's involvement with ***in situ* conservation** projects, ranging from the Freshwater Fish Conservation Program[11] in Madagascar to

---

[10] St Louis is pronounced, at least by the people who live there, as Saint LOO-ISS, not Saint LOO-EY.

[11] Program and Programme are, respectively, the American and British spellings of the same word
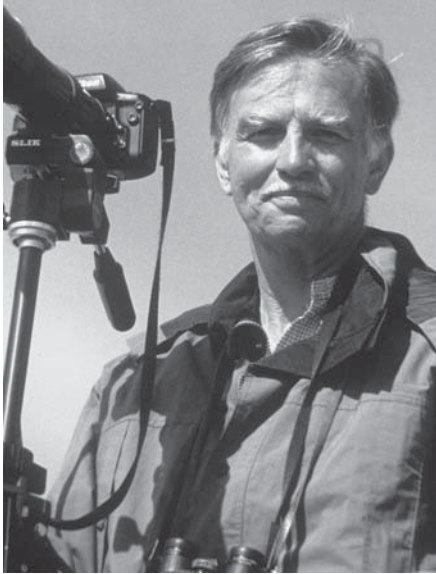
Figure 2.15 William (Bill) Conway, formerly General Director of the New York Zoological Society and President of the Wildlife Conservation Society. (Photograph: AZA)

monitoring populations of endangered primates in Africa. By 1999, when Conway retired, the WCS was pursuing more than 350 conservation programmes in fifty-two nations. In the year of his retirement from the presidency of the WCS, the AZA created the William Conway Chair for Conservation Science, in recognition of Conway's enormous contribution to wildlife conservation and, in particular, his lead in showing how zoos could support *in situ* conservation projects.

On the other side of the Atlantic, one of the most influential zoo directors of the twentieth century was Gerald Durrell, known initially as an author (with best-selling books such as *My Family and Other Animals* to his name), who founded Jersey Zoo in the Channel Islands. The now world-famous zoo at Les Augres Manor in Jersey opened officially in 1959. Like Conway, Durrell was ahead of his time with his emphasis on conservation and the captive breeding of endangered species from around the world. In 1963, Durrell incorporated the Zoo into a new charitable trust,

the Jersey Wildlife Preservation Trust. This was followed in the 1970s by the creation of an International Training School for young conservationists. To date, more than 3,000 students and conservationists from around the world have benefited from the experience of a placement and training at Jersey Zoo.

With Durrell's death in 1995, the Trust was renamed the Durrell Wildlife Conservation Trust, and Gerald Durrell's work has been continued by his widow, Lee. Today, the Trust is involved in efforts to save a wide variety of endangered species, particularly **island endemics**,[12] ranging from the mountain chicken *Leptodactylus fallax* from Montserrat and Dominica in the Caribbean (this species is a frog, not a bird), to the Lesser Antillean iguana *Iguana delicatissima*.

Finally, David Hancocks is a Zoo Director Emeritus who has paid tribute to Conway and Durrell as inspirational leaders of zoos. Author of *A Different Nature: The Paradoxical World of Zoos and Their Uncertain Future* (Hancocks 2001), David Hancocks trained as an architect in Britain, and went on to run three highly regarded zoos: Woodland Park Zoo in Seattle, the Arizona-Sonora Desert Museum, and most recently, Werribee Open Range Zoo near Melbourne in Australia, where he now lives. His is often a critical voice within the zoo profession. At a recent symposium on '*The Future of Zoos*' (more on this in **Chapter 15**), he said:

> 'There is urgent need for zoos to pay closer attention to the interconnectedness between living things … there is equally vital need to improve the welfare standards of all beings in their care. … There is, too, great need for zoos to broaden their skills by adding scientists in senior positions, particularly ecologists and geologists with their characteristically wide and deep views on nature.'
>
> (Hancocks 2012).

We agree!

---

[12] An **island endemic** is a species that is native and confined to an island or group of islands. Examples include the aye-aye *Daubentonia madagascariensis* and other lemur species on Madagascar, which originate from Madagascar and are not found in the wild anywhere else in the world.

Bronx Zoo in New York and Gerald Durrell at Jersey Zoo, who were at the forefront of the drive to put wildlife conservation at the top of the zoo agenda.) Many lost, or tried to lose, the name 'zoo' along the way, with varying degrees of success. For example, the Bronx Zoo became the 'International Wildlife Conservation Park' for a while in the 1990s, but has now abandoned the struggle and reverted to the name by which it has always been widely and popularly known.

Safari parks

The first safari park to open in the UK (in 1966) was at Longleat, in Wiltshire (with the claim of being the first safari park to open outside Africa). Woburn, in Bedfordshire, followed soon after, in 1970. The safari park concept was promoted initially in the UK by circus director Jimmy Chipperfield, who persuaded both the Marquess of Bath at Longleat, and then the Duke of Bedford at Woburn, to enter into a partnership with him to develop large drive-through paddocks and enclosures, housing (mainly) African animals such as giraffes (**Fig 2.16**), lions, and rhinoceroses.

Australia was quick to see the potential of what we call safari parks in the UK, and which are often known as open range zoos in Australia. Examples are Taronga Western Plains Zoo, which opened in 1977, and, more recently, Werribee Open Range

Figure 2.16 The first safari parks opened in the 1960s and 1970s. This photograph shows visitors (disregarding Park instructions to keep their car windows closed) and giraffes in one of the drive-through enclosures at Midlands Safari Park, UK. (Photograph: Robek/CC-BY-SA).

Zoo (part of the Zoos Victoria group) which offers an African safari experience.

Landscape immersion

In the 1970s, the Woodland Park Zoo in Seattle, USA, under the directorship of David Hancocks (see **Box 2.5**), employed the architects Jones and Jones to help to develop a plan to renovate the zoo. For the first time, the visitors and the animals were brought together in the same habitat—it was the advent of **landscape immersion** (Hancocks 2001). Instead of wandering around a city park looking at replicas of desert, or savannah, or rainforest habitats, zoos visitors walked *through* the rainforest, with the animals and rainforest plants (or replicas of rainforest plants) all around them.

The move towards more naturalistic exhibits was not always welcomed at first, either by the paying visitors or by the zoo employees. Well into the 1970s, it was believed, for example, that attempts to house gorillas in exhibits with live vegetation were doomed to failure: the animals would simply destroy the plants or would injure themselves falling out of trees (Hancocks 2001). The pioneering new gorilla enclosure at Woodland Park Zoo, Seattle, which opened in 1978, showed other zoos what could be done. Not only could gorillas safely be housed in large outdoor enclosures with natural vegetation and even tall trees, but both the gorillas and the visitors could benefit from the experience (Hancocks 2001; see also Embury 1992).

The concept of landscape immersion has now been adopted by other zoos, although not as rapidly and widely as some might have hoped. Hancocks (2001) gives as other examples of **immersion exhibits** the gorilla enclosures at Zoo Atlanta in Georgia, USA, and at Melbourne Zoo in Australia, as well as the African savannah exhibit at Disney's Animal Kingdom in Florida. Other good examples can be seen at Burgers' Zoo, Arnhem (**Fig. 2.17**), in the Netherlands. Within the UK, examples of landscape immersion exhibits are Bristol Zoo's Seal and Penguin Coasts, and Paignton Zoo Environmental Park's Desert House.

Figure 2.17 This photograph shows visitors at Burgers' Zoo, Arnhem, in the Netherlands, exploring an immersion exhibit. This style of exhibit is designed to make visitors feel as though they are immersed in the animals' natural habitat. (Photograph: Andrew Bowkett)

Ecosystem exhibits and bioparks

An ecosystem exhibit is designed to represent an entire ecosystem, rather than a single species or a group of animals displayed on taxonomic or regional lines (see **Box 2.6**). In the USA in particular, the trend towards exhibiting animals within a portrayal of their ecosystem is known as the biopark (or 'BioPark') concept and has been promoted by, among others, Michael Robinson, director of the Smithsonian's National Zoo in Washington, DC. Robinson (1996a,b) explains that '*a bioexhibit should portray life in all its interconnectedness*'. In other words, in a biopark or ecosystem zoo, the plants, as well as the animals, are integral to the exhibit and the overall aim is to demonstrate the interdependencies between the living things in a particular ecosystem. Of course, a realistic portrayal of '*life in all its interconnectedness*' would also include predators and predation, but this is not always fully possible in the zoo environment, other than perhaps allowing some natural foraging for invertebrate prey.

Hancocks (2001) cites as a good example of an ecosystem exhibit the Louisiana Swamp at the Audubon Park Zoo in New Orleans. Here, the plants, animals, and people that live in the swamps of southern Louisiana are combined into an exhibit that extends to more than two hectares, with black bears, turtles, raccoons, otters, and alligators dispersed among the swamp cypresses and lagoons. In Europe, the Masoala Rainforest exhibit at Zurich Zoo has

An 'ecosystem zoo' or 'ecosystem exhibit' is one that attempts to recreate or provide information about an entire ecosystem, not only the animals and plants that live within it. An ecosystem comprises both living organisms and their non-living environment, such as the rainfall, and the rocks and soils. A modern example of an ecosystem exhibit is the Masoala Rainforest at Zurich Zoo, in Switzerland. This is an award-winning greenhouse ecosystem within which temperature, humidity, and 'rainfall' are carefully controlled to match, as closely as possible, natural conditions in a Madagascar rainforest (**Plate 2.1**). The plants are an integral part of the exhibit, not just a backdrop to the animals.

been widely praised (**Fig. 2.18**, **Plate 2.1**, and **Box 2.6**). This 11,000m^2 greenhouse ecosystem, which opened in 2003, promotes the

Figure 2.18 The Masoala Rainforest Hall was opened in 2003 at Zurich Zoo and represents a contemporary approach that brings together native flora and fauna in one exhibit. In this exhibit, visitors are transported to a 'real-life' Madagascan experience. (Photograph: Zurich Zoo)

species diversity of the Masoala National Park in Madagascar and also contributes to raising funds (currently more than US$100,000 p.a.) for *in situ* conservation initiatives in the National Park (Bauert *et al.* 2007).

The first ecosystem zoo in the USA (see **Table 2.1** for some other notable 'firsts' in the zoo world) did not open under the name 'zoo'. The Arizona-Sonora Desert Museum, which opened in Tucson, Arizona, in 1952, set out to be a 'living museum' of the plants and animals of the Sonora Desert. Each enclosure represented a particular habitat and signage provided information on the entire ecosystem (Kisling 2001). These innovations were widely copied by other zoos in the latter half of the twentieth century.

Zoos in the twenty-first century

So how are zoos likely to evolve from here? What will be the defining characteristics of zoos in the twenty-first century? We have tried to address some of these questions in the final chapter of this book (**Chapter 15**). We are already beginning to see the advent of the sustainable zoo, or at least a greater focus by zoos on **sustainability** in all of their operations. But before considering, in the final sections of this chapter, the philosophy and ethics of zoos, and how modern zoos see their role at the start of the twenty-first century, it is worth pausing to look specifically at the history of aquariums and how this differs from the history of zoos.

Date	Initiative/development	Zoo/location
1793/ 1828	First openings of a major public zoo as part of a scientific institution	The Jardin des Plantes, Paris, France, as part of the Museum of Natural History (1793) London Zoo in Regent's Park, London, UK, under the umbrella of the Zoological Society of London (ZSL) (1828)
1847	Word 'zoo' first appears in the *Oxford English Dictionary*	A reference to Clifton 'Zoo', Bristol, UK, and, later, an abbreviation of the Zoological Gardens in London, UK
1849	Opening of first reptile house	London Zoo, UK
1853	Opening of first public aquarium	London Zoo, UK
1906	First birth of an elephant (Asian elephant *Elephas maximus*) in captivity in a zoo in Europe	Tiergarten Schönbrunn, Vienna, Austria
1907	First scientific zoo journal launched (*Zoologica*)	Published by the US New York Zoological Society
1938	First oceanarium opens in USA (displaying marine mammals)	Marineland, St Augustine, Florida, USA
1938	First children's zoo	London Zoo, UK
1943	First duck-billed platypus *Ornithorhynchus anatinus* bred in captivity	Healesville Sanctuary, near Melbourne, Australia
1952	First ecosystem zoo opens in USA	Arizona-Sonora Desert Museum, Tucson, Arizona, USA
1953	First nocturnal house at a zoo	Twilight World, Bristol Zoo Gardens, UK
1963	First giant panda *Ailuropoda melanoleuca* cubs born in captivity (as a result of artificial insemination)	Chengdu Giant Panda Breeding Research Centre,* China
1966	First safari park outside Africa opens	Longleat, Wiltshire, UK
1978	First 'landscape immersion' exhibit opens, at an American zoo	Gorilla World, Woodland Park Zoo, Seattle, USA
2001	Birth of first test-tube elephant (an African elephant *Loxodonta africana*, named Abu) in captivity	Tiergarten Schönbrunn, Vienna, Austria
2006	First captive-bred giant panda released back into the wild	Wolong Giant Panda Protection and Research Centre, China
2011	First hellbenders[13] *Cryptobranchus alleganiensis* born in captivity	Saint Louis Zoo, Missouri, USA

Table 2.1 Some notable 'firsts' in the history of zoos and aquariums

*Now the Wolong Giant Panda Protection and Research Centre.

[13] Hellbenders are giant salamanders. The Ozark hellbenders which were bred in captivity at Saint Louis Zoo are listed in the IUCN 'red list' as near-threatened (Hammerson and Phillips 2004).

2.4 The history of aquariums

Public aquariums are a more recent phenomenon than public zoos (see **Table 2.2** for the dates of opening of some of the world's best-known zoos and aquariums), although brightly coloured ornamental fish have been kept in captivity in ponds and containers (both natural and artificial) for centuries, particularly in Asia (Kisling 2001).

From the nineteenth century onwards, advances in the manufacture of glass tanks allowed fish to be viewed from the side, rather than only from above when in ornamental ponds (Hoage

and Deiss 1996). London Zoo was the first zoo to capitalize on this new technology, with the opening of the world's first public aquarium, known as the 'Vivarium' or 'Fish House', in 1853. The following extract from a newspaper of the day (the *Literary Gazette*) gives some idea of the impact of the opening of the Fish House:

'A living exhibition of the sea-bottom and its odd inhabitants is such an absolute novelty, that we must give our readers … some account of the elegant aquatic vivarium just opened to the public.'

(Kisling 2001)

Date of opening	Zoo or aquarium	Location
1245	Tower Menagerie *(closed in 1832)*	London, UK
1800	Exeter 'Change (Exchange) *(closed in 1828)*	London, UK
1752	Tiergarten Schönbrunn *(Vienna Zoo)*	Vienna, Austria
1793	Jardin des Plantes	Paris, France
1828	London Zoo *(part of the Zoological Society of London, or ZSL)*	Regent's Park, London, UK
1830	Dublin Zoo	Dublin, Republic of Ireland
1835	Bristol Zoo	Bristol, UK
1838	Natura Artis Magistra *(Artis Zoo)*	Amsterdam, Netherlands
1843	Antwerp Zoo	Antwerp, Belgium
1844	Zoologischer Garten *(Berlin Zoo)*	Berlin, Germany
1858	Diergaarde Blijdorp *(Rotterdam Zoo)*	Rotterdam, Netherlands
1861	Melbourne Zoo	Melbourne, Australia
1864	Moscow Zoo	Moscow, Russia
1868	Lincoln Park Zoological Gardens *(Chicago Zoo)*	Chicago, IL, USA
1873	National Aquarium	Washington, DC, USA
1874	Philadelphia Zoo *(the first zoological park to open in the USA)*	Philadelphia, PA, USA
1889	National Zoo of the United States *(Smithsonian National Zoological Park)*	Washington, DC, USA
1899	Bronx Zoo	New York, NY, USA
1907	Hamburg Tierpark *(Hagenbeck's Tierpark)*	Hamburg, Germany

Date of opening	Zoo or aquarium	Location
1913	Royal Zoological Society of Scotland Zoo (*Edinburgh Zoo*)	Edinburgh, Scotland
	Burgers' Zoo and Safari	Arnhem, Netherlands
1916	Taronga Zoo	Sydney, Australia
1923	Paignton Zoo Environmental Park (*Paignton Zoo*)	Paignton, UK
1928	Münchener Tierpark (*Munich Zoo*)	Munich, Germany
1931	Chester Zoo	Chester, UK
	Zoologická zahrada Praha (*Prague Zoo*)	Prague, Czech Republic
1934	Belfast Zoo (*originally Bellevue Zoo*) Duisburg Zoo	Belfast, UK Duisburg, Germany
1937	Dudley Zoo	Dudley, UK
1956	Dierenpark Planckendael (*Planckendael Zoo*)	Mechelen, Belgium
1959	Durrell Wildlife Conservation Trust (*Jersey Zoo*)	Jersey, Channel Islands
1963	Colchester Zoo	Colchester, Essex, UK
	Twycross Zoo	Twycross, UK
1964	Sea World	San Diego, CA, USA
1970	Vancouver Zoo	Vancouver, BC, Canada
1971	Apenheul Primate Park	Apeldoorn, Netherlands
1972	Marwell Wildlife (*Marwell Zoo*)	Hampshire, UK
1974	Toronto Zoo (*Riverdale Zoo in Toronto was open from 1894 to 1974*)	Toronto, Canada
1981	The National Aquarium	Baltimore, MD, USA
1984	Monterey Bay Aquarium	Monterey, CA, USA
1986	The Seas with Nemo and Friends (*previously The Living Seas*)	Orlando, FL, USA
1998	National Marine Aquarium	Plymouth, UK
	Disney's Animal Kingdom	Orlando, FL, USA
	Blue Planet (*aquarium*)	Ellesmere Port, Cheshire, UK
2002	The Deep (*aquarium*)	Hull, UK
2005	Georgia Aquarium (*currently the world's largest aquarium, although Osaka also claims this title*)	Atlanta, GA, USA
2012	Riverboat Safari, Singapore	Singapore

Table 2.2 Dates of opening of some major zoos and aquariums in Europe, North America, and Australia*

*After Kisling (2001), who provides a detailed and comprehensive list of chronological information about the zoos and aquariums of the world.

Given that the tanks had to be aerated by hand-operated pumps, the Fish House was home to a remarkable variety of species, with more than sixty species of fish and more than 200 different marine invertebrates on display (Barrington-Johnson 2005). The Fish House lasted until the early twentieth century, by which time the popularity of keeping marine and freshwater fish in tanks had waned.

In much the same way that the Jardin des Plantes in Paris had prompted the opening of other 'new' zoological gardens in Europe, the Fish House at London Zoo led to the development of aquariums elsewhere in the UK and in mainland Europe. Among these is the Stazione Zoologica aquarium in Naples, Italy, which opened to the public in 1874. This is one of only a handful of nineteenth-century aquariums still open to the public (it is now part of an internationally important multidisciplinary biological research centre); another aquarium that has partially survived from this time is in Brighton in Sussex, now open as a Sea Life Centre.

The first public aquarium in the USA was opened in 1856, as part of the American Museum in New York, by Phineas T. Barnum (the same Barnum whom, as we saw earlier in this chapter, acquired Jumbo the elephant from London Zoo for exhibit in his circus). The first **oceanarium** in America, displaying marine mammals, opened in 1938 (see **Table 2.1**). This was Marineland, in St Augustine, Florida. Other marine mammal parks followed in towns and cities across Europe and the USA, although a few were short-lived and closed again soon after opening (for example, Marineland of the Pacific, in California, which was open from 1954 until 1987). The 1970s and 1980s, in particular, saw an expansion in the number of centres holding marine mammals for public display, although increasing concern for the welfare of these animals in captivity has seen a decline in recent years in the number of **dolphinariums** and oceanariums in the UK and, to a lesser extent, elsewhere.

In contrast to the decline in oceanariums, the past two decades or so have seen great

Figure 2.19 In much the same way as we have described advances in terrestrial captive animal exhibitory, similar advances have also been made in the display of aquatic animals. Here, you can see one of the large tanks at The Ocean, the aquarium at Burgers' Zoo at Arnhem, in the Netherlands, which houses a diversity of fish and other marine fauna. (Photograph: Julian Doberski)

modernization of aquariums (**Fig. 2.19**), and also the opening of a number of impressive and popular new aquariums, from Monterey Bay Aquarium in California (1984) (**Plate 2.2**) to Océanopolis in Brest, in France (1990), and The Deep, in Hull (2002) in the UK (see **Tables 2.1** and **2.2**). Warwick Frost, in his book *Zoos and Tourism* (Frost 2011), points out that there has been a recent trend to include aquariums in tourism-focused developments, and attributes this in part to their relatively modest space needs. He cites as examples the Aquarium of the Bay in San Francisco, and Underwater World in Singapore, on the resort island of Sentosa.

2.5 Zoos today

It is almost impossible to generalize about zoos today. Whether or not you believe that zoos are a force for good will depend both on your attitudes towards keeping wild animals in captivity (more on this in the next section) and on what type of zoo you are considering. At one end of the scale, there are zoos such as the Durrell Wildlife Conservation Trust (Jersey Zoo) or Chester Zoo (both in the UK), or the Bronx Zoo in New York, with

very high standards of animal welfare and husbandry, and a genuine and strong commitment to wildlife conservation. At the other end of the scale, there are far too many appalling 'roadside zoos' in far too many countries around the world, where animals languish in pitifully small cages, with very low standards of welfare.

As Hancocks (2001) has said:

'The history of zoos is replete with contradictions. People have set up zoos because they wanted to control big strong animals … in recent years there are increasing numbers of people who want to work in zoos because they are passionate about wildlife conservation.'

But regardless of your personal beliefs, there is no getting away from the fact that zoos are numerous, highly popular, and almost certainly here to stay. So what is—or rather, what should be—the role of the modern zoo?

2.5.1 How does the modern zoo see its role?

In common with many organizations nowadays, zoos attempt to articulate their perceptions of their role and purpose through various positioning statements, aims, objectives, or mission statements. These identify what the zoo thinks its purpose is, what perspective it looks from, and what it particularly values in achieving that purpose. These statements are usually published for all to see on the zoos' websites, and a review of a number of these is sufficient to show that most are concerned with education, conservation, and providing a valuable experience for visitors.

A typical example is Chester Zoo in the north of England, which states as its vision and mission:

'Our vision is for a diverse, thriving and sustainable natural world … our mission is to be a major force in conserving biodiversity worldwide'

The Los Angeles City Zoo website has the simple banner heading, '*Nurturing Wildlife and*

Enriching the Human Experience'. And Taronga Zoo, in Sydney, has as its mission statement, '*We will demonstrate a meaningful and urgent commitment to wildlife, our natural environment and the pursuit of excellence in our conservation, recreation and scientific endeavours*' (**Fig. 2.20**).

These are all medium- to large-sized zoos with high visitor numbers, substantial animal holdings and resources that can be channelled into research, and *in situ* conservation (that is, conservation in the animals' habitat countries). But even smaller zoos espouse the same priorities. To consider only one, Shaldon Wildlife Park in Devon is just an acre in size (and the smallest member of BIAZA and EAZA); its stated mission is '*To be a proactive contributor to the preservation of the wildlife of the planet*'. Overall, then, zoos see—or at least say that they see—their primary purposes as being involved in the conservation of endangered species, and helping to foster public appreciation and interest in the natural world.

In many countries, zoos may belong to a national or regional association or federation of zoos. The aims and mission statements of these associations differ in some respects from those of their constituent zoos, in that they emphasize the fostering of between-zoo cooperation and the maintenance of high professional standards. However, the priorities they stress are the same ones: namely, conservation, education, welfare, and research.

In the UK and the Republic of Ireland the relevant association is The British and Irish Association of Zoos and Aquariums (BIAZA). (There is more information about zoo associations in **Chapter 3**, which looks at the legislative and regulatory framework for zoos.) BIAZA's mission states that it '*represents its members and promotes the values of good zoos and aquariums*'. Among other objectives, it leads and supports its members '*to inspire people to help conserve the natural world*' and '*to participate in effective cooperative conservation programmes*'.

The equivalent to BIAZA in the USA is the Association of Zoos and Aquariums (AZA). Its mission is very similar to that of BIAZA, as are

Figure 2.20 This highly complex and large gibbon enclosure provides its inhabitants with the structural features necessary to perform **brachiation**[14] and many other species-specific behaviours necessary to the maintenance of their general health and welfare. Alongside this enclosure, in Sydney's Taronga Zoo, information panels highlight the need to conserve this species in the wild, and provide information to the visiting public about how they can contribute to the Zoo's conservation activities. (Photograph: Julian Chapman)

those of other similar associations elsewhere in the world.

So we might summarize the majority view of modern zoos—or at least accredited zoos—as being that they see themselves as agencies for undertaking conservation. They do this through their collections and, in an increasing number of cases, through conservation work in the wild as well—and they also use their collections for education and raising awareness about the natural world. Of course, the rather cynical response to this would be that zoos in many countries now have a statutory obligation to demonstrate that they are involved in conservation, and it would

be surprising if their activities and mission statements did not reflect this.

But would zoos still exist if the paying public were not able to see exotic animals at first hand? As Michael Robinson, Director of the Smithsonian's National Zoo in Washington, DC, points out, zoos are fundamentally:

> '…. places of spectacle and entertainment. Research, education and conservation are functions which, in the last one hundred years or so, have been grafted onto the recreational rootstock of zoos.'
>
> (Robinson 1996a)

And this brings us to philosophical questions, such as whether or not zoos *should* exist. Under what circumstances is it ethically justifiable to keep wild animals in captivity?

---

[14] **Brachiation** is a movement seen in animals such as gibbons, which involves swinging from arm to arm through the trees.

2.6 The philosophy and ethics of zoos

Because of the charge that zoos are involved in keeping animals captive for the purposes of human recreation and entertainment, questions may be asked about the ethics of what zoos do and their underlying philosophy (see **Box 2.7** for a brief explanation of what is meant by 'ethics'). For example, on what grounds can we justify keeping wild animals in captivity (**Fig. 2.21**)? How should zoo directors respond to the charge, from animal rights campaigners and others, that zoos are morally indefensible? And how should zoos approach the ethical paradox that conservation is all about species and populations, but welfare is about individual animals?

2.6.1 Should zoos exist?

The American philosopher Dale Jamieson (1995) has argued that there is a '*presumption for liberty*' and that it is morally wrong to deprive animals of their freedom by keeping them in captivity. As Stephen Bostock (1993) points out, we condone the loss of liberty for humans only under very specific and limited circumstances (such as a prison term as punishment for law-breaking).

Box 2.7   WHAT DO WE MEAN BY 'ETHICS'?

The words 'morals' and 'ethics' are often used together, and, in some cases, as though they mean the same thing. The *Concise Oxford Dictionary*, for example, defines ethics as '*relating to morals; treating of moral questions; morally correct, honourable*' (Sykes 1977). But are ethics and morals really the same thing? Before we can consider any ethical or moral concerns in relation to keeping wild animals in captivity in zoos, we need to be clear about exactly what we mean by these terms.

Many people will freely express moral concerns about keeping animals in captivity, whether in zoos, or as pets, or on farms, or in the laboratory, but often the moral positions that people take may be contradictory or inconsistent. For example, some people may believe that it is wrong to keep dolphins or killer whales in captivity, but perfectly acceptable to keep tropical fish in a small tank in the living room at home. Most people in the UK would think it was wrong to throw stones at a sleeping lion in a zoo to wake it up, but in other parts of the world such behaviour might be encouraged by other visitors rather than frowned upon.

In other words, moral concerns and beliefs are an individual's view of what is right or wrong, and may result from careful thought about the underlying issues, or may just be based on a 'gut feeling' about whether or not something is acceptable (Straughan 2003). As Straughan points out, ethics is a narrower concept than morality, and refers to a branch of philosophy that tries to clarify and analyse the arguments that people use when discussing moral questions. This involves probing the justifications that we have for believing that some things are right and other things are wrong.

So a good general description of ethics might be '*a set of standards by which a particular group of people decides to regulate its behaviour—to distinguish between what is legitimate and acceptable in pursuit of their aims, from what is not acceptable*' (Flew 1979). Of course, different people have different moral outlooks and approach ethical decisions in different ways. For this reason, the recommendation of the UK *Zoos Expert Committee Handbook* (Defra 2012b; see the Defra website at **http://www.defra.gov.uk**) is that zoos should set up and utilize ethical committees rather than leave ethical decisions to individual people. The *Handbook* provides advice on how to set up appropriate ethical panels, in both large and small zoos, together with suggestions on the types of member that such panels should have.
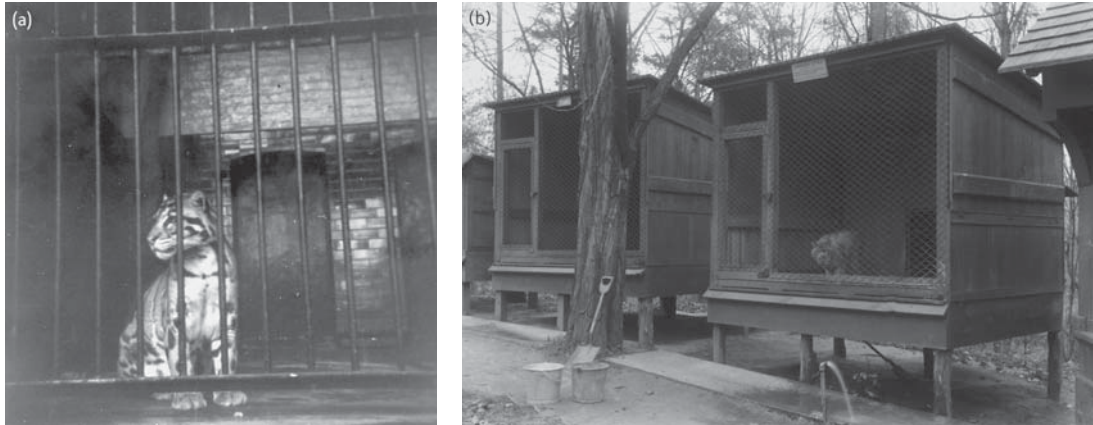
Figure 2.21 When some people argue against the notion of keeping wild animals captive in zoos, it is possible that they may have a preconception that animals are still housed in cages like the one illustrated in (a). This cage housed a clouded leopard *Neofelis nebulosa* at London Zoo in the 1960s and the cage design has clearly not greatly advanced from the sort of cage used to house lynx *Lynx* spp. (b) at the Smithsonian's National Zoo in the early years of the last century. It should be clear from reading this chapter so far that zoo design has progressed greatly since this time, and that these images are thankfully reminiscent of a past that is no longer present in good zoos. (Photographs: (a) Geoff Hosey; (b) Smithsonian's National Zoo)

Bostock (1993) summarizes the three main arguments in defence of keeping wild animals in captivity as follows:

- keeping wild animals in captivity has advantages for humans (education, conservation, recreation, scientific discovery) and sometimes for the animals themselves as well (conservation can be viewed as beneficial for populations of animals, if not always for individual animals kept in captivity);
- wild animals in captivity may not necessarily experience negative welfare and may, in some cases, be better off than they would be in the wild;
- animals are not sufficiently comparable to humans to make meaningful comparisons about the morality of captivity.

The first of these arguments reflects a broadly **utilitarian** approach to the question of whether or not wild animals should be kept in captivity (see **Box 2.8** for an explanation of terms such as **utilitarianism**). The last two arguments are essentially about animal rights.

DeGrazia (2002) makes an important distinction between *captivity* and *confinement*, and argues that confinement '*restricts liberty in a way that significantly interferes with one's ability to live well*'. By this definition, the confinement of wild animals (for example, in very small barren cages) has the capacity to cause harm, but captivity *per se* does not.

The animal rights viewpoint: are zoos morally indefensible?

Tom Regan is a leading American philosopher who is the author of two influential books: *The Case for Animal Rights* (1983) and, with Peter Singer, *Animal Rights and Human Obligations* (1976, reprinted 1999). Regan (1995) has considered whether or not ethical viewpoints such as utilitarianism and the animal rights view (see **Box 2.8**) can be used to make the case that zoos are morally indefensible. He comes to the, perhaps surprising, conclusion that none of the main ethical theories can be used as the basis of a watertight argument that zoos are morally indefensible. Even the animal rights view, which Regan strongly supports and which, as he says, '*takes a very dim view of zoos*' (Regan 1995), cannot be used to argue against zoos in the (admittedly limited) circumstances under which it can be demonstrated that it is in the best interests of an animal to be kept in captivity for a period of time. He illustrates this with the example of an

Box 2.8　UTILITARIANISM AND ANIMAL RIGHTS

Before we can consider the impact of the animal rights movement on the zoo world, we need to understand some of the language and approaches used by writers and philosophers when discussing this area. The idea behind utilitarianism is that we should act so as to produce the greatest good or 'utility' for the largest number of individuals (put crudely, 'maximum gain for minimum pain'). Utilitarians view the suffering of animals (such as rats and mice undergoing medical experiments in a laboratory) as acceptable, provided that the benefits to humans (for example, a cure for a disease) outweigh the costs to the animals (Appleby and Hughes 1997). Of course, measuring the costs to the animals in this sort of case is far from straightforward.

In contrast with utilitarianism, animal rights campaigners generally hold that the rights of animals are equivalent to those of humans and that it is never acceptable to sacrifice the interests of one animal to benefit another. Peter Singer, the author of *Animal Liberation* (1990), is a strong proponent of the utilitarian viewpoint; another well-known philosopher, Tom Regan, is a proponent of the animal rights viewpoint. Some philosophers believe that we unthinkingly value benefits to humans more than costs to animals; this human tendency is referred to by Singer as **speciesism** (Appleby and Hughes 1997).

The animal rights movement is a relatively recent phenomenon. It has developed over the past three or four decades, out of various human rights movements (it is worth noting that the General Assembly of the United Nations set out its Universal Declaration of Human Rights as recently as 1948). Most animal welfare organizations now hold that animals do have certain rights, or entitlements, but that these are not equivalent to those of humans.

animal that would be killed by humans if it were to be allowed to remain in its natural habitat.

This short summary is only a very simplistic representation of Regan's conclusions in relation to zoo animals and does not give a full picture of his views on animal rights. We strongly recommend that readers with an interest in the ethics of keeping wild animals in zoos should read for themselves other books and essays on environmental ethics, several of which are listed in **Further reading** at the end of this chapter.

Other dilemmas for zoos

The animal rights view espoused by Regan and others is, of course, not the only critical view of zoos. Bertram (2004) provides a useful list of the main criticisms of zoos, and considers whether or not each of these criticisms is valid. Others have argued that zoos give a false and compromised picture of habitats and ecosystems by concentrating on larger species—and particularly mammals—at the expense of the smaller species that make up a vital part of a functioning ecosystem (Hancocks 1995).

There is certainly much truth in this criticism, but zoos are gradually moving towards collections that reflect a more representative sample of the natural world and are also prioritizing keeping threatened species, not only examples of the (largely mammalian) **charismatic megafauna** (**Fig. 2.22**). This debate is revisited and expanded on in **Chapter 10** on 'Conservation'.

Other arguments against zoos include their cost, with the usual suggestion being that the money spent on running a zoo would be better spent directly on *in situ* conservation. However, zoos tend to meet most of their running costs from the entrance fees paid by visitors ('gate money'), and there is no evidence that the public would give this money to conservation projects if zoos did not exist. A stronger argument is that it is often more cost effective to conserve animals in the wild, and increasingly the better zoos are supporting a range of field projects that do just this (and of course these initiatives are supported by the gate money that comes from the zoo visitors).

Figure 2.22 Nothing better characterizes the concept of the 'charismatic megafauna' than a large animal that people find inspiring and exciting. The Asian rhino *Rhinoceros unicornis*, pictured here at Warsaw Zoo, epitomizes a species that would encourage many people to visit the zoo. (Photograph: Warsaw Zoo)

Zoos are by no means the only organizations that face these sorts of dilemma: ethical concerns can arise from a very wide range of activities in which humans come into contact with animals (notably farming). But this book is about zoos, so what are the other ethical issues that zoos need to address? Zoos face issues about the acquisition, transfer, and disposal of animals: for example, under what circumstances is it acceptable for zoos to acquire animals from the wild? Nowadays, and particularly in Europe, North America, and Australia, most animals in zoos were born in captivity. Routine management procedures in zoos can have an impact on welfare; the training of animals to facilitate routine husbandry tasks may also have welfare implications. These and other ethical issues for zoos are addressed in the following sections of this chapter, and also in **Chapter 7** on Welfare.

Conservation versus welfare?

The genetic management of zoo animals to reduce **inbreeding** and to maintain **genetic diversity** may require the sterilization of some animals, or their removal from breeding groups. This highlights another moral dilemma: as zoos shift their focus towards achieving conservation goals, they may find that these goals come into conflict with the provision of high standards of welfare for individual animals (the tension between the conservation

of species and populations, and the welfare needs of individual animals is discussed further in **Chapter 7**). There are strong moral arguments on both sides, but there is clearly the potential for conflict between these two imperatives. Jamieson (1995) has said that '*conflicts of value are intrinsic to wildlife management*', but goes on to say that just because these conflicts exist does not mean that we cannot make better decisions, nor that we are excused from reflecting on how they can be resolved.

Ethical guidelines for zoos

Support for zoos in resolving these and other ethical issues comes from bodies such as the Zoos Expert Committee in the UK, and from zoo associations. BIAZA, for example, has published an Animal Transaction Policy that, among other things, identifies good practice in the acquisition, transfer, and disposal of animals. Similarly, the North American zoo association the AZA has published policies on the acquisition and disposal of animals and on other issues, as has the Zoo and Aquarium Association (ZAA) in Australia. Zoo associations such as the European Association of Zoos and Aquaria (EAZA) have also been vocal in their calls for greater government intervention to deal with 'bad zoos' (there is more about this in **Chapter 15**).

2.6.2 Anti-zoo campaigns

The 1960s and 1970s onwards saw, both in the USA and Europe, the emergence of a new generation of animal rights and animal welfare organizations concerned either specifically or peripherally with zoos. The first group of zoo animals to be targeted was the marine mammals. Captive killer whales *Orcinus orca* and other members of the dolphin family attracted much attention in the 1970s, 1980s, and 1990s.

More recently, elephants have moved up the agenda. The publication in the UK of a study (Clubb and Mason 2002) commissioned by the Royal Society for the Prevention of Cruelty to Animals (RSPCA) drew attention to a number of health and welfare issues relating to elephants in

captivity in zoos. This was followed in 2008 by a report from academics at Bristol University, commissioned and part-funded by Defra (Harris *et al.* 2008), which raised similar concerns. In particular, Harris *et al.* (2008) drew attention to problems of foot health, gait, and obesity in elephants in UK zoos. The Zoos Forum (2010), now replaced by the Zoos Expert Committee, provided a clear and succinct review of the 2008 report, and suggested a number of ways in which the zoo community could and should address concerns about the welfare of elephants in their care. In response to one of the main recommendations made by the Zoos Forum, for the setting up of an independent Elephant Advisory Group, BIAZA set up the Elephant Welfare Group (in 2010) with a remit to take forward a number of evidence-based steps to improve the welfare and husbandry of zoo elephants in the UK.

In the USA, activists from organizations such as People for the Ethical Treatment of Animals (PETA) and the Humane Society of the United States have joined forces with local pressure groups over recent years, to try to remove elephants altogether from a number of AZA zoos (Donahue and Trump 2006). The activists argue that elephants should not be kept in small enclosures or small social groups, but should instead be sent to sanctuaries where they can roam in larger groups over a much larger acreage of land. This has happened in a number of cases, notably with the opening in 1995 of The Elephant Sanctuary in Tennessee in the USA; this facility extends to more than 1,000ha. Of course, the public may not always be able to visit these sanctuaries to see the elephants.

Similar campaigns in Europe have been instigated by groups such as the Born Free Foundation, Care for the Wild, and Animal Defenders, and some anti-zoo campaigners have argued that all animals should be removed from zoos (see McKenna *et al.* 1987). In 2009, the Born Free Foundation (an independent campaigning organization which operates under the stated mission '*to phase out zoos*') initiated a survey of a sample of zoos across Europe. The findings were published under the title of *The EU Zoo Inquiry 2011*. The stated aim of these visits was to assess compliance of zoos across Europe with the EU Zoos Directive (European Council Directive 1999/22/EC; see **Chapter 3**). Despite its title, however, this inquiry was not conducted by the EU nor one of its agencies, but by representatives from the Born Free Foundation and from another campaigning organization, ENDCAP (End Captivity, a coalition of animal welfare organizations in Europe).

The Zoo Check programme (part of the Born Free Foundation) states explicitly on its website that '*wild animals do not belong in zoos*' and operates under the slogan '*Keep Wildlife in the Wild*'. Unfortunately, it is simply not feasible for all the people who currently visit zoos each year to travel to see the same animals in the wild. As Bostock (1993) has put it: '*millions of people … could never, in comparable numbers, visit "the wild" without damaging it irreparably*'. And, to the suggestion that zoo visitors could view wildlife films or virtual exhibits rather than live animals, Donahue and Trump (2006) offer the response that '*their consistently high attendance at zoos indicates that they do not desire to replace zoos with television shows*'.

Summary

• The history of captive collections of exotic animals is a very long one, dating back at least 4,000 years. Some of the earliest records of collections of wild animals in captivity come from Egypt, Mesopotamia, China, and Greece.

• In the nineteenth century, scientific societies set up leading European zoos such as the Jardin des Plantes and London Zoo.

• In contrast, twentieth-century zoos, particularly in the USA, were usually municipal (civic) institutions.

• The so-called 'Disinfectant Era' of the early part of the twentieth century saw the introduction in many zoos of easy-to-clean, but sterile, cages with tiled walls, smooth concrete floors, and steel doors.

• Zoo exhibits in the second half of the twentieth century have become more naturalistic, with a new generation of bioparks, ecosystem exhibits, and landscape immersion exhibits that do not focus only on a single species, but rather on animals in their natural environments.

• In the latter half of the twentieth century, zoos began to face organized opposition from a new generation of animal rights and animal welfare organizations.

• Many zoos, at least partly in response to criticism from animal rights campaigners, have reinvented themselves as conservation organizations.

• At the start of the twenty-first century, the best zoos are retaining their emphasis on conservation, and are also striving to become sustainable organizations and environmental centres.

Questions and topics for further discussion

1. Under what circumstances is it ethically acceptable to keep wild animals in captivity?
2. Are zoos a force for good in modern society?
3. What brought about the so-called Disinfectant Era or Hygiene Era in Western zoos? What are the advantages and disadvantages of this approach to captive animal management?
4. Why should zoos display ecology rather than taxonomy?
5. Discuss the following statement: '*Landscape immersion exhibits are good for visitors but not for animals*'.
6. Who should own zoos? Are zoos best managed at national or at city level, as public bodies or as private institutions?
7. What should be done about 'roadside zoos'? Should all zoos that do not belong to a formal zoo association such as BIAZA, EAZA, AZA, or ZAA be closed down?

Further reading

The history of zoos

Accounts of zoo history abound, both in print and on various websites, but be warned that not all of these are accurate. We strongly suggest that anyone with a keen interest in zoo history checks, for themselves, wherever possible, the original sources.

For a detailed and thoroughly researched account of the history of zoos around the world, we recommend both Kisling's *Zoo and Aquarium History* (2001) and Baratay and Hardouin-Fugier's *Zoo: A History of Zoological Gardens in the West* (2004). Kisling's book is more global in its scope and considers the history of zoos in other parts of the world, such as the Aztec and Inca collections which, for reasons of space, have not been included in this chapter. It has a comprehensive reference list at the end for anyone wanting to delve still further into the records of the animal collections of ancient Egypt, or Greece, or Rome. For anyone wanting to learn more about the keeping (and killing) of wild animals during the days of the Roman Empire, Carcopino (1991) provides a vivid account of daily life in ancient Rome; George Jennison's classic, *Animals for Show and Pleasure in Ancient Rome*, first published in 1931, was reprinted in 2005 and is now available in paperback (Jennison 2005).

Another comprehensive account of zoo history is provided by Hoage and Deiss (1996), the editors of *New Worlds, New Animals: From Menagerie to Zoological Park in the Nineteenth Century*. Several of the chapters in this book are based on papers presented at a symposium on zoo history, held at the National Zoo in Washington in 1989. For an account of the history of US zoos, Elizabeth Hanson's *Animal Attractions: Nature on Display in American Zoos* (2002) is well worth reading, and features an interesting chapter on the history of wild animal collectors and zoo expeditions over the past century. Another recommended read is Nigel Rothfels' *Savages and Beasts* (2002). Rothfels traces the birth of the modern zoo to Hagenbeck's influence, and offers much detailed information about both Hagenbeck and the creation of the Hamburg Tierpark.

In the introduction to *A Different Nature: The Paradoxical World of Zoos and Their Uncertain Future* (2001), David Hancocks provides a good overview of zoo history, as does Stephen Bostock in his

book on *Zoos and Animal Rights* (1993). An even shorter, but nevertheless recommended, summary of zoo history is found in the 'Foreword' written by Michael Robinson, the Director of the Smithsonian's National Zoological Park, in Washington, DC, for Hoage and Deiss (1996).

Finally, even if you are not a herpetologist, do not be put off by the title of James Murphy's *Herpetological History of the Zoo and Aquarium World* (2007). This hefty book covers many aspects of zoo and aquarium history, and, although there is plenty about amphibians and reptiles in the book, there is also much information of general interest.

The philosophy and ethics of zoos

The basics

In an excellent booklet produced for the Biotechnology and Biological Sciences Research Council (BBSRC), Roger Straughan (2003) gives a clear and concise explanation of the difference between moral and ethical concerns, and goes on to provide short summaries of topics such as animal **sentience** and speciesism (this booklet is available on the BBSRC website). Although the booklet is entitled *Ethics, Morality and Animal Biotechnology*, much of the content is relevant in a wider context. Straughan also poses the question 'What is an animal?' and rightly points out that you cannot fully consider animal ethics without first deciding what counts as an animal. For an introduction to animal rights, David DeGrazia's affordable book provides a good overview of the key issues (DeGrazia 2002), although the author admits to not having visited some of the zoos he discusses. We also recommend Armstrong and Botzler's *The Animal Ethics Reader* (2003).

Further reading on the philosophy and ethics of zoos

Four books on the philosophy and ethics of zoos stand out. Firstly, although it is a challenging read in places, we recommend *Ethics on the Ark: Zoos, Animal Welfare and Wildlife Conservation*, written and edited by Bryan Norton and his colleagues (1995). This includes chapters from moral philosophers such as Tom Regan and Dale Jamieson (although, frustratingly, this book lacks an index). More challenging still, but recommended nonetheless, is the book edited by Singer and Regan, *Animal Rights and Human Obligations* (1976, reprinted 1999), although some of the examples of poor practice in zoos cited by, for example, James Rachels (1976) in this book are now more than half a century old. Stephen Bostock, a zoologist and philosophy student who went on to work at Glasgow Zoo, has produced a much more accessible account of the history and philosophy of zoos in his book, *Zoos and Animal Rights* (1993). Finally, we recommend David Hancock's thoughtful and well-written text, *A Different Nature: The Paradoxical World of Zoos and Their Uncertain Future* (2001).

For a readers wanting a shorter overview of some of the key ethical issues facing zoos, Michael Kreger and Michael Hutchins (Kreger and Hutchins 2010) provide a useful and current review of ethical issues in the specific context of keeping mammals in zoos and aquariums.
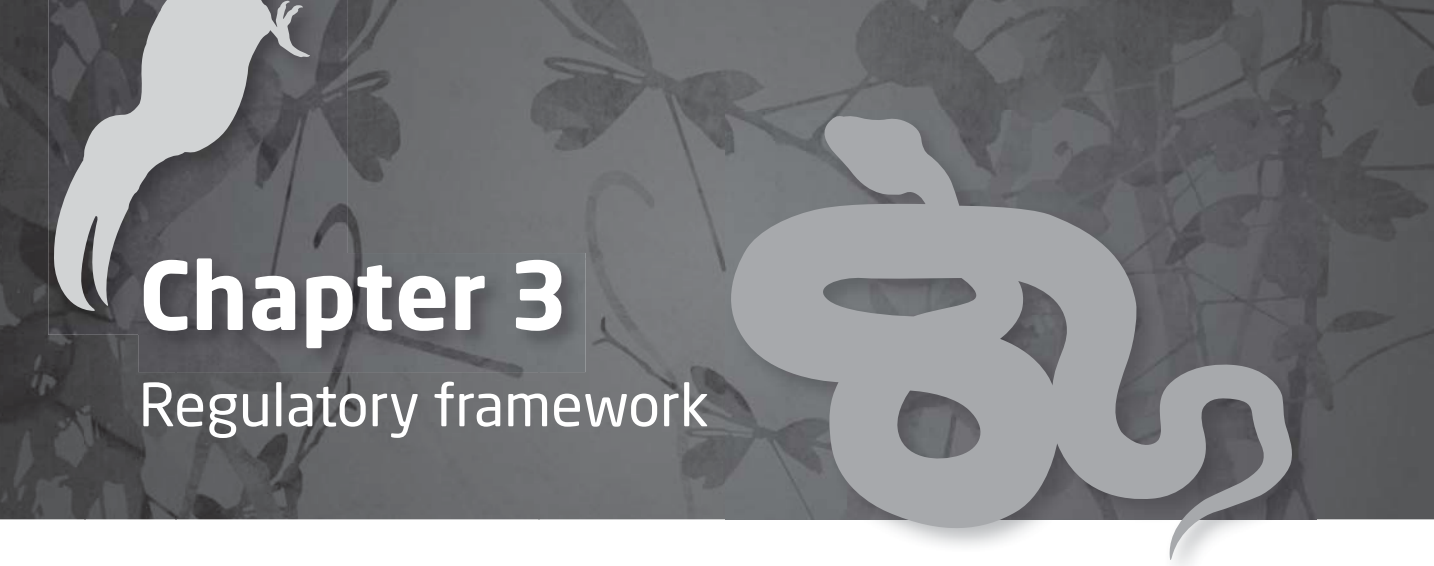
Zoo politics

Jesse Donahue and Erik Trump's *The Politics of Zoos: Exotic Animals and Their Protectors* (2006) is essentially a political biography of the American Association of Zoos and Aquariums (now known as the AZA). It is a book that offers detailed and useful insights into how zoos in the USA responded to the growing challenge from animal rights and animal welfare organizations in the latter half of the twentieth century.

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.
http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Chapter 3
Regulatory framework

Zoos operate within a complex framework of conventions, directives, laws, procedures, policies, regulations, and recommendations. This framework extends from international agreements through to regional, national, and sub-national (for example, state) legislation and guidelines. The extent and influence of the legislative and regulatory framework varies considerably from country to country and from region to region. Much of what will be described in this chapter relates to the legal framework for zoos within Europe, and within the UK in particular, but many other countries have similar operating frameworks.

The main topics that we will cover in this chapter are as follows.

3.1	**The law and legislative processes: a brief introduction**
3.2	**The international framework: global conventions, agreements, and regulations**
3.3	**Zoo legislation within the European Union**
3.4	**The regulatory framework for zoos in the UK: legislation and guidelines**
3.5	**Zoo legislation outside Europe**
3.6	**Zoo associations: from BIAZA and EAZA, to AZA, ZAA, and WAZA**

Tables and boxes in this chapter provide additional information, such as a summary of key international conservation treaties and organizations (**Table 3.1**) and an overview of devolved legislation within the UK (see **Box 3.2**). As in other chapters, acronyms are defined on first use (and are also listed at the start of the book).

Given the dynamic nature of legislation, some of the information provided in this chapter is likely to become out of date quite quickly. Web addresses can also change, as can the names or acronyms for national and international organizations. Other than checking all information at the time of writing, which we have done, there is little else that we can do except to add a caveat that readers should check the relevant websites for any updates. There is a section at the end of this chapter with details of where to go for further information.

3.1 The law and legislative processes: a brief introduction

Before considering the laws within which zoos operate, let us first briefly consider the law and legislative processes in general.

Laws are the rules that govern society. These rules set out both the rights and the responsibilities of citizens. Legislation is needed to ensure that people can live together safely and peacefully, and to enforce good practice. Sometimes guidelines and persuasion are not enough to ensure compliance with sensible welfare or safety precautions in zoos.

But a law is only effective if it can be implemented; there are many examples, both current and historic, of 'bad laws' that are difficult to enforce and are widely flouted.

3.1.1 Civil and criminal law

In most countries in the English-speaking world, 'the law' is divided into civil law[1] and criminal law. Offences under criminal law can be punished by a jail sentence or a fine and the offender, once proved guilty, will have a criminal conviction. Offences under civil law determine liability for harm, rather than guilt, and are not punishable by a prison sentence, but damages may be payable. Liability in a civil court is decided on the 'balance of probabilities' rather than under the tougher criterion of 'beyond reasonable doubt' that is used for criminal law. (This applies to the law in the UK, the USA, and Australia, for example, but not in all countries.)

Enforcement also differs between criminal and civil law. Criminal law is enforced by officers of the state bringing a criminal action. In the UK, criminal law is enforced by the police and, in England and Wales, by the Crown Prosecution Service (CPS). The equivalent of the CPS in Scotland is the Crown Office, and in Northern Ireland, the Public Prosecution Service. A zoo in the UK could face criminal proceedings, for example, under the provisions of the Animal Welfare Act 2006. Breaches of civil law, on the other hand, are enforced by people or organizations with an interest in the case (for example, a person who has suffered harm) bringing litigation in the civil courts. Another example would be if a civil action were to be initiated because an individual or an organization believed that breaches of regulations controlling the operation of a zoo had occurred. Such a civil action may not necessarily be taken directly against a zoo, but could be taken against a third party, such as a local council, for permitting a zoo to continue operation when it has not complied with licensing requirements.

3.1.2 Legislative processes at international and national levels

The laws governing the operation of zoos can be considered at three main levels: global or international, regional (for example, European), and national. Countries such as the USA and Australia also have state or territory legislation at sub-national level, and many countries have local regulatory or licensing arrangements that augment national laws, such as local government by-laws in the UK (Cooper 2003). Although the regulatory framework for zoos varies considerably between different countries, Cooper (2003) points out that there are some basic elements that are common across much zoo legislation, such as the requirement for authorization to open and operate a zoo (for example, via a licence or permit), processes for zoo inspections before a licence or permit is granted, and a set of minimum standards that must be met. Zoos are also often required by law to keep certain types of record.

There is no body that makes international laws that are binding on all of the nation states of the world. Instead, various international organizations (such as the United Nations) propose treaties and conventions, which individual countries may or may not choose to sign or 'join'. But once such treaties are incorporated into national law, they are every bit as binding as other national legislation.

Within Europe, the European Union (EU) can pass legislation that is binding on all member states, although this depends on the category of EU legislation that is put forward. There are three main categories of EU legislation:

- EC Regulations are directly binding upon member states;
- EC Directives are not directly binding on member states, and need to be incorporated into national legislation before they can take effect;
- EC Decisions are binding on member states, but are limited in scope (these come from either the European Commission or the European Council).

---

[1] The term 'civil law' also refers to a type of legal system that is in widespread use today. Also known as European Continental Law, the civil law system is largely derived from Roman law.

Box 3.1   A BRIEF GUIDE TO THE EUROPEAN UNION

What is now the European Union (EU) started life as the European Economic Community (EEC) in 1957, with the signing of the Treaty of Rome by France, West Germany, Italy, Belgium, the Netherlands, and Luxembourg. After 1967, the EEC became the European Community (or, more correctly, the European Communities), generally known as the EC. The UK joined the EC in 1973. After the Maastricht Treaty of 1993, the EC became part of the wider EU.

Confusingly, the European Commission, which is part of the EU (essentially, it is the EU's 'civil service'), is also sometimes referred to by the abbreviation 'EC'. And to add to the possible confusion, EC can also be the acronym for the European Council, which is a body made up of the heads of government of the EU member states, along with the President of the European Commission and the President of the European Council. If you really need to know whether a particular piece of EU legislation has come from the Commission or the Council, this is stated in full on the legislation, all of which is available online.

The presidency of the EU rotates between its member states every six months (the EC Zoos Directive, adopted in 1999, was a significant achievement of the UK presidency in the preceding year).

It is worth noting that the original Treaty of Rome, founding what has now become the EU, did not include any reference to animal welfare. A revision of the Treaty some 40 years later resulted in the signing of the Treaty of Amsterdam in 1997; this did include a Protocol on animal welfare.

Further information about the EU and EU law can be found online at the official website of the European Union (**http://europa.eu/**).

You may be wondering why EU legislation is often preceded or followed by the letters EC (as above, in EC Directives). **Box 3.1** provides a short explanation, and a brief guide to the EU.

In the UK, primary legislation is made via Acts of Parliament. There is also secondary legislation, which is not debated in Parliament and which therefore can be amended more rapidly. EC Directives are often implemented within the UK as secondary legislation (the 2002 Regulations amending the Zoo Licensing Act 1981 (ZLA),[2] which is considered later in this chapter, are a good example of secondary legislation). Some UK legislation is implemented by setting out specific standards, which can be changed and updated by the Secretary of State. It is also worth noting that not all of the UK Acts mentioned in this chapter have power in all of the UK's constituent countries; **Box 3.2** provides details of devolved legislation in Northern Ireland, Scotland, and Wales.

[2] Zoo Licensing Act 1981 (Amendment) (England and Wales) Regulations 2002, SI 2002/3080.

3.2 The international framework: global conventions, agreements, and regulations

Examples of international conventions that impact on the operation of zoos include the 1973 Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (UN 1973), the 1992 Convention on Biological Diversity (CBD) (UN 1992), and the Berne Convention, which covers the conservation of European wildlife and habitats. (See Holst and Dickie (2007), for a review of conservation conventions and agreements that influence zoos.)

A wide range of other international organizations, standards, and guidelines have some influence on how zoos operate, including the Food and Agriculture Organization (FAO), the International Union for Conservation of Nature (IUCN), and the United Nations Environment Programme (UNEP). All of this can be a bit bewildering at first if you are not familiar with these various bodies and organizations, but **Table 3.1**

Box 3.2 DEVOLVED ZOO LEGISLATION WITHIN THE UK

Scotland, Wales, and Northern Ireland often have their own versions of UK and European laws. In 1999, Scotland acquired its own Parliament; the same year saw the creation of the Welsh Assembly, with more limited devolved legislative authority.

Some UK legislation relating to zoos, such as that stemming from the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (UN 1973), is not devolved, but in other areas it is, and so zoos at different locations within the UK may have to meet different legal requirements for some aspects of their operation. The Animal Welfare Act 2006,

for example, applies only to England and Wales. Scotland has its own Act: the Animal Health and Welfare Act (Scotland) 2006 (see **http://www. scotland.gov.uk** for further information). Where UK legislation is devolved, the full title of the Act makes this clear by naming the constituent countries to which the Act applies. So while the Zoo Licensing Act 1981 applies throughout the UK, the Zoo Licensing Act (Amendment) (England and Wales) Regulations 2002 apply only within England and Wales.

In practice, the devolved legislation is usually broadly similar across the UK.

Acronym	Full name	Role	Further information
CBD	United Nations Convention on Biological Diversity (often referred to as the Convention on Biodiversity)	The CBD was one of the main outcomes of the 'Earth Summit' at Rio de Janeiro in Brazil in 1992.	**http://www. cbd.int** Montreal, Canada (**Fig. 3.1**)
CBSG	Conservation Breeding Specialist Group (part of the IUCN) (Before 1994, the CBSG was the Captive Breeding Specialist Group)	The CBSG, set up in 1979, was created to provide a link between the IUCN and zoos.	**http://www. cbsg.org** Apple Valley, MN, USA
CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora	CITES is a trade convention, not a conservation convention. The CITES Secretariat is administered internationally by the United Nations Environment Programme.	**http://www. cites.org** Geneva, Switzerland (**Fig. 3.1**)
FAO	Food and Agriculture Organization of the United Nations	The FAO, established in 1945, has a mandate to work to '*defeat hunger*'. Its remit includes improvement of agriculture, forestry, and fisheries practices. The work of the FAO covers domestic animal transport and diseases such as avian influenza (H5N1).	**http://www. fao.org** Rome, Italy

Acronym	Full name	Role	Further information
IUCN	International Union for Conservation of Nature	The IUCN issues guidelines and policy positions and statements (e.g. guidelines on species reintroduction) on wildlife conservation and also on the sustainable use of natural resources. The IUCN is perhaps best known for its 'Red List' of species at risk of extinction.	http://www. iucn.org Gland, Switzerland
OIE	Office International des Epizooties (World Organisation for Animal Health)	The OIE, created in 1924, monitors and disseminates information on animal disease worldwide via its website and periodicals, and other publications.	http://www. oie.int Paris, France
SSC	Species Survival Commission (of the IUCN)	The Species Survival Commission is a network of experts who (on a voluntary basis) advise the IUCN on issues relating to conservation. It has a number of specialist groups, such as the coral reef fish group and the equids group.	http://www. iucn.org/ species Gland, Switzerland
TRAFFIC	TRAFFIC is not an acronym, but the name of a joint programme of WWF and the IUCN	TRAFFIC exists to monitor trade in wild plants and animals, and to reduce the threat of such trade to conservation. It works in close cooperation with the CITES Secretariat.	http://www. traffic.org Cambridge, UK
UNEP	United Nations Environment Programme	UNEP, established in 1972, describes itself as '*the voice for the environment within the United Nations system*'.	http://www. unep.org Nairobi, Kenya
WCMC	United Nations Environment Programme World Conservation Monitoring Centre	UNEP–WCMC is the biodiversity assessment and policy implementation arm of UNEP.	http://www. unep-wcmc.org Cambridge, UK
WTO	World Trade Organization	The WTO was established in 1995 as the successor to the General Agreement on Tariffs and Trade (GATT) and deals with the global rules of trade between nations.	http://www. wto.org Geneva, Switzerland
WWF	Since 2000, WWF has been known only by its acronym, which originally derived from 'World Wildlife Fund', and then 'World Wide Fund for Nature'	WWF is an independent wildlife conservation organization and a charity that promotes and supports the conservation of both species and habitats. Founded in the UK in 1961, it is now a major international organization.	http://www. panda.org (The website for WWF in the UK is http://www. wwf.org.uk)

Table 3.1 Major international conservation organizations and conventions (in alphabetical order)

Note: Web addresses shown in this table were correct at the time of publication—but can change. An online search under the full name of any one of these organizations should take you to its current website.

explains all these acronyms and provides brief details about each international organization or convention, together with website addresses for finding further information, and **Figure 3.1** illustrates the interrelationships between two major international conventions or treaties and regional and national law governing how zoos operate.

(a)

UN Convention on Biodiversity (CBD)
www.cbd.int
Set up at the 'Earth Summit' in Rio de Janeiro in 1992,
the CBD requires Parties to engage in ex-situ conservation

EU Zoos Directive 1999
Council Directive 1999/22/EC of 29 March 1999

Article 1 Definition of a zoo	Article 3 Implementation of conservation measures	Article 4 Zoo licensing and inspection	*Other Articles (there are 11 in total) cover topics such as the closure of zoos*

Article 3, on conservation measures, includes education (compulsory) and captive breeding (optional). *Each EU member state is required to engage in one or more of four optional areas of activity, including research, training, information exchange and/or captive breeding and reintroduction*

Article 4, on licensing, requires that *'Every zoo shall have a licence within four years after the entry into force of this Directive or, in the case of new zoos, before they are open to the public'.*

Implementation of the EU Zoos Directive into national legislation in EU member states: examples

Austria Animal Protection Law, Federal Law Gazette N° 118/2004	**Denmark** Order N° 1023 (zoos),	**Germany** BGBl I 2002, 1193 Nature Conservation and Landscape Management	**Italy** Decreto Legislativo n°73, 21/03/05 (zoos)	**United Kingdom** Zoo Licensing Act 1981

(b)

Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) 1973
www.cites.org
CITES is a trade convention, not a conservation convention. The Secretariat of CITES is administered by the United Nations Environment Programme.

Within Europe, CITES is implemented by **Council Regulation (EC) No. 338/97 of 9th December 1996 on the protection of species of wild fauna and flora by regulating trade therein**
For the purposes of CITES, the EU is regarded as a single state

CITES: Appendices *The appendices to CITES are lists of endangered species for which trade is controlled, with species in Appendix I being considered at greatest risk*	**EU : Annexes** *There are four annexes (A-D) to the EU legislation implementing CITES*
Appendix I *Examples of species include all the great apes, such as the gorillas and chimpanzees*	Annex A *This includes all CITES Appendix I species, as well as some Appendix II and III species for which the EU has adopted stricter measures*
Appendix II *Species listed in Appendix II are not considered to be under current threat of extinction, but could become so unless trade is closely controlled (eg. the saiga antelope)*	Annex B
Appendix III	Annex C
	Annex D

Within the UK, the relevant domestic legislation for CITES is the Control of Trade in Endangered Species (Enforcement) Regulations 1997 (the COTES Regulations), as amended in 2005

Figure 3.1 Diagram (a) shows the relationship between an important international convention, the United Nations Convention on Biological Diversity (CBD), and regional and national law governing the licensing and activities of zoos within Europe. Diagram (b) sets out the relationship between another international convention or treaty, the Convention on Trade in Endangered Species of Wild Fauna and Flora (CITES), and EU and UK legislation. Other European countries within the EU have similar legislation to the UK's COTES Regulations.

3.2.1 The 1973 Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)

CITES was set up in 1973 at a meeting of representatives of eighty countries in Washington, DC, to discuss the regulation of wildlife trade for conservation purposes. CITES entered into force in 1975. Countries or states ('parties') that agree to be bound by CITES are said to have 'joined' CITES and must implement the Convention via their own national legislation (**Fig. 3.1**).

CITES is an important international agreement, but it is, first and foremost, a trade agreement, not primarily conservation legislation. There are some highly endangered species, for example, in which there is little international trade. CITES is of limited relevance for these species. The major impact of CITES on zoos is the requirement for permits for the movement of animals (or animal parts or tissues) belonging to species listed by CITES as endangered or threatened. As Cooper and Cooper (2007) point out, however, prosecutions under CITES frequently involve offences in other areas as well, such as breaches of animal welfare or animal health legislation in the case of illegal transport of wild animals.

Approximately 5,000 animal and 25,000 plant species are listed in three appendices to CITES (see http://www.cites.org). These appendices are amended and updated in biennial Conferences of the Parties (CoPs). Appendix I of CITES covers species that are deemed to be at highest risk—that is, those that are threatened with extinction and which may be affected by trade. For these species, trade is permitted only under exceptional circumstances.

Appendix I species include the great apes (the bonobo or pygmy chimpanzee *Pan paniscus*, the common chimpanzee *Pan troglodytes*, the gorillas *Gorilla* spp., and the orang-utans *Pongo* spp.), as well as the Asian and African elephants *Elephas maximus* and *Loxodonta africana* (the African elephant populations of Botswana, Namibia, South Africa, and Zimbabwe are included in Appendix II rather than Appendix I, as these populations are deemed to be at lower risk). Avian species listed

Figure 3.2 The Waldrapp, or northern bald ibis *Geronticus eremita* is listed in Appendix I of CITES. (Photograph: Sheila Pankhurst)

under Appendix I include the Waldrapp or northern bald ibis *Geronticus eremita* (**Fig. 3.2**); notable reptilian species listed in Appendix I include the Komodo dragon *Varanus komodoensis*.

Appendix II of CITES lists species that are not considered to be under current threat of extinction, but which could become so unless trade is closely controlled. An example (**Fig. 3.3**) is the saiga antelope *Saiga tatarica* (although it is worth noting that the saiga is included in the Zoological Society of London's list of EDGE species—those that are '*evolutionarily distinct and globally endangered*').

Figure 3.3 The saiga antelope *Saiga tatarica* is listed in Appendix II of CITES. This is an example of a species that is not considered to be under current threat of extinction, but which could become so unless trade is closely controlled.

The operation of CITES within the European Union

For the purposes of CITES, the EU is regarded as a single state and, within Europe, CITES is implemented via Regulation (EC) No. 338/97. This Regulation is legally binding on all EU member states.[3] Within each nation state, there is a CITES Management Authority, which has an administrative role, and which deals with the practicalities of issuing permits for the transport of animals and animal parts. There is also a CITES Scientific Authority in each state; this has an advisory role.

Within the UK, the relevant domestic legislation for CITES is the Control of Trade in Endangered Species (Enforcement) Regulations 1997 (the COTES Regulations), as amended in 2005 to increase the penalties for illegal trading in endangered species. The UK government's Department for Environment, Food and Rural Affairs (Defra) is the CITES Management Authority in the UK and has responsibility for issuing permits for the movement of animals (and animal body parts and tissues) covered by CITES. The **Joint Nature Conservation Committee (JNCC)**[4] is the CITES Scientific Authority (Fauna) within the UK and has an advisory role.

Because the EU is effectively a single state in relation to CITES, the movement of endangered species within the EU is relatively free (at least in relation to the Convention). However, there are some EU amendments to the CITES appendices or lists of endangered species. These are published in four EU Annexes to CITES, known as Annexes A, B, C, and D. Annex A includes all CITES Appendix I species, as well as some Appendix II and III species for which the EU has adopted stricter measures. (For example, the barn owl *Tyto alba* (**Fig. 3.4**) is an **Annex A species** but is listed in CITES Appendix II, rather than Appendix I.)

Figure 3.4 The European Union has its own Annexes to CITES legislation. An example of an Annex A species that is not listed on CITES Appendix I is the barn owl *Tyto alba*. (Photograph: Liam Kite)

A permit known as an **Article 10 certificate** is needed by zoos within the EU to authorize the commercial use of animals listed under Annex A (displaying animals to the public is deemed commercial use). The **Websites and other resources** section at the end of this chapter gives details of a useful summary from TRAFFIC of EU animal trade legislation and required documentation.

Some European zoos have an **Article 60 certificate** (formerly an 'Article 30 certificate') which allows them to display their Annex A species and also to move them to other zoos within the EU, provided that the other zoos also have an Article 60 certificate. Further information can be found on the Defra website (**http://www.defra. gov.uk/**).

For animal species listed under EU Annexes A and B, permits require minimum standards for transport and housing (and animals moved under this legislation must be microchipped). Annex A animals that are captive bred rather than wild captured (that is, second generation, or **F2**, zoo animals) may, under some circumstances, be able to be moved to Annex B and then

---

[3] Within Europe, CITES legislation is implemented under criminal, not civil, law and transgressions can result in imprisonment or a fine.

[4] The **Joint Nature Conservation Committee (JNCC)** is the official or statutory adviser to the UK government on conservation issues (see **http://jncc.defra.gov.uk**).

be transported more easily. Satisfying the CITES definition of 'captive bred' is not as straightforward as it might seem, however. All the following criteria must be met:

- specimens must have been born or produced in a controlled environment;
- the parents must have mated (or gametes must have been transferred) in a controlled environment;
- the breeding stock must have been established and maintained in accordance with CITES Resolution Conf. 10.16 (Rev.).

Production of a second generation

Zoos wishing to move captive-bred (F2) Annex A animals under Annex B must be able to prove that they have met all the above criteria. They can do this, for example, by reference to records maintained by the International Species Information System (ISIS) (see **section 5.7.1**). In addition, animals moved under this legislation must be clearly marked, usually with a microchip.

3.2.2 The 1992 Convention on Biological Diversity (CBD)

Another international convention that impacts on zoos is the Convention on Biological Diversity (CBD), often just referred to as the Convention on Biodiversity (**Fig. 3.1**). Signed by 150 government leaders at the UN 'Earth Summit'[5] held in Rio de Janeiro, Brazil, in 1992, the CBD is dedicated to promoting sustainable development. The CBD is an important convention and is the international umbrella for the 1999 EC Zoos Directive (see next section).

The text of the CBD refers to ***in situ*** and ***ex situ* conservation**[6] measures and Article 9 of the Convention specifically requires that:

'Each party shall … adopt measures for the ex-situ conservation of components of biological diversity …, establish and maintain facilities for ex-situ conservation of plants, animals and micro-organisms, preferably in their country of origin…'
(EC 2006)

The EU and its member states, via the EC Zoos Directive, can refer to zoo conservation work to indicate compliance with the CBD.

3.2.3 The International Air Transport Association (IATA) Live Animal Regulations (LARs)

Like CITES and the CBD, membership of the International Air Transport Association (IATA) is voluntary. Airlines, rather than nation states, choose to become members of IATA and, once they have joined, must abide by IATA's Live Animal Regulations (LARs) (IATA 2012). These regulations are intended to ensure that live animals are transported safely, legally, and with good standards of welfare. Copies of LARs are available both as a book and in digital format, and provide information and detailed specifications in areas such as crate size and ventilation (see **http://www.iata.org/**). IATA membership now extends to more than 200 international airlines; LARs are enforced within the EU, and are also officially recognized by organizations such as CITES and the World Organisation for Animal Health (OIE),[7] as well as by many individual countries.

Additional guidance on the international transport of live animals is available from the Animal

---

Transportation Association (ATA) (see **http://www.ata-animaltransport.org**). This is a voluntary organization that works closely with the IATA.

3.2.4 Other international agreements, guidelines, and regulations

As Holst and Dickie (2007) point out in their review of national and international regulations influencing zoos, there is '*an overwhelming array of conventions and regulations whose sole purpose is to protect wildlife and regulate wildlife trade, constituting a complex legal framework with which zoos must comply*'.

Two important areas that we have not yet considered in this chapter are international regulations and standards on animal health and disease, and guidelines on the **reintroduction** of animals into the wild. The following sections provide a very brief overview of these topics, with details of where to find further information.

Animal health and disease

The World Organisation for Animal Health (OIE) produces standards that are widely used by government veterinary agencies as a key source of information about the prevention and management of outbreaks of animal disease. OIE publications include the *Terrestrial Animal Health Code*, which is published annually, and the *Aquatic Animal Health Code* (information on both these Health Codes can be found on the OIE website).

Reintroduction of animals into the wild

In 1995, the International Union for Conservation of Nature (IUCN) approved a set of guidelines on the reintroduction of wild animals and plants (IUCN/SSC 1998). These guidelines are still widely used today and form the basis for many **taxon**- or species-specific reintroduction plans (reintroduction is considered in more detail in **Chapter 10** on 'Conservation'). The website of the British and Irish Association of Zoos and Aquariums (BIAZA) provides a useful overview to the IUCN guidelines for reintroduction (**www.biaza.org.uk**).

Some of the key criteria listed in the IUCN guidelines are:

- the species must have been a former inhabitant of the area;
- the causes of extinction must be known and must no longer exist;
- there must be suitable habitat available;
- reintroduction should be monitored carefully.

3.3 Zoo legislation within the European Union

The main legislation governing the operation of zoos within the EU is the 1999 EC Zoos Directive[8] (**Fig. 3.1**). There is a wide range of other EU legislation that impacts on zoos, including Regulations governing the transport and welfare of animals, and also issues such as carcass disposal (animal by-products legislation).

3.3.1 The EC Zoos Directive

For countries that are members of the EU, the EC Zoos Directive of 1999 (Council Directive 1999/22/EC) was a major step forward in European legislation governing zoos and resulted in the closure in some countries of some very poor zoos. The EC Zoos Directive sets out requirements for the licensing and inspection of zoos, for proper record-keeping, and for standards of animal care. The Directive also requires zoos to participate actively in education and conservation. Zoos that are not directly involved in captive breeding or species reintroduction programmes can meet the conservation requirement of the EC Zoos Directive by undertaking or supporting conservation-related research and training, although, as Rees (2005a) has pointed out, the CBD already requires parties to engage in all of these activities.

---

[8] The full title of the Zoos Directive is Council Directive 1999/22/EC of 29 March 1999 relating to the keeping of wild animals in zoos.

It should be noted that not all EU member states (for example, Spain) met the April 2002 deadline for incorporating the EC Zoos Directive into their national legislation (Stevenson 2010).

3.3.2 Other EU legislation governing how zoos operate

Transport

The IATA LARs have already been mentioned (see **section 3.2.3**) and these are enforced throughout the EU. In addition, Council Regulation (EC) No. 1/2005 on the protection of animals during transport is directly binding on member states (this is a Regulation rather than a Directive). In the UK, this EU legislation is enacted via the Welfare of Animals (Transport) (England) Order 2006, and other similar legislation in Wales, Scotland, and Northern Ireland.

The Balai Directive

The **Balai Directive** is an EU Council Directive (92/65/EEC) that governs the transport of non-domestic animals between EU member states, with respect to veterinary screening and animal health.

Balai was approved in 2002 as a 'catch-all' Directive for a range of animals not covered by other EU legislation and governs the movement not only of live (wild) animals, but also of semen, ova, and embryos.

The original Balai Directive (92/65/EEC) has since been amended by Council Directive 2004/68/EC.

Obtaining Balai approval involves a considerable amount of work for zoo vets and managers. Once in place, however, Balai approval is intended to allow easier movement of animals between the zoo and other approved institutions (**Fig. 3.5**). For example, non-Balai-approved premises within Europe can no longer import or export any primate species, and approval from the State Veterinary Service (SVS),[9] or its equivalent for each country, must be sought before other animals can be transferred to a non-Balai-approved zoo. New animals from non-Balai-approved zoos or other sources must go into isolation for a period of 30 days after importation into an approved zoo.

Although the aim of the Balai Directive is to make it easier to transfer animals between approved premises such as zoos for legitimate purposes such as conservation programmes, in practice it is '*difficult veterinary legislation*' (Dollinger 2007). In a

Figure 3.5 Transport between zoos of animals such as (a) the sea otter *Enhydra lutris* and (b) the gharial *Gavialis gangeticus* is covered in Europe by the Balai Directive; zoos that are 'Balai approved' can exchange animals more easily. (Photographs: (a) Jeroen Stevens, and (b) Smithsonian's National Zoo)

[9] The State Veterinary Service in the UK merged with other services in 2007 to become an agency known as Animal Health. A further merger took place in 2011, resulting in the creation of the Animal Health and Veterinary Laboratories Agency (AHVLA). see the Defra website (**http://www.defra.gov.uk**) for more details.

review of the Balai Directive, Peter Dollinger, Executive Director of the World Association of Zoos and Aquariums (WAZA), commented:

> 'Because of time constraints, Directive 92/65 was prepared hastily and without consulting with the zoo community. It was poorly drafted, in particular its English version, and thus unclear, misleading and impractical.'
>
> (Dollinger 2007)

Waste management

Another EU Regulation that impacts on the operation of zoos is EU Regulation No. 1069/2009 and accompanying Implementing Regulation (EC) 142/2011. This legislation, which came into force in 2011, regulates how animal by-products are used, and allows some controlled feeding of zoo herbivores to zoo carnivores where there is not deemed to be any health risk from doing so. The 2009/2011 Regulations have replaced rather more restrictive previous legislation (Animal By-Products Regulation (EC) No. 1774/2002), which caused some consternation to zoos previously accustomed to 'feeding in' dead animals (for example, feeding a dead goat to a lion or a tiger).

3.4 The regulatory framework for zoos in the UK: legislation and guidelines

The most important legislation governing zoos within the UK is the Zoo Licensing Act 1981 (ZLA), as amended in 2002, but this Act is by no means the only UK legislation regulating how zoos operate. For example, the Animal Welfare Act 2006 impacts on zoos, as does legislation on animal health, human health, animal transport, and a whole host of other areas. In this section, we will look first at the ZLA and then at other legislation governing zoos in the UK.

3.4.1 The Zoo Licensing Act 1981

Within the UK, the EC Zoos Directive is implemented via the Zoo Licensing Act 1981, as amended by the Zoo Licensing Act 1981 (Amendment) (England and Wales) Regulations 2002 (HMSO 2002). The ZLA was first passed in 1981, some 18 years prior to the EC Zoos Directive, but has been updated and strengthened more recently to reflect the requirements of the EC Zoos Directive, particularly in relation to conservation and education work by zoos (Kirkwood 2001a). This Act was one of the earliest articles of legislation in Europe to set out requirements for a system of zoo inspection (Stevenson 2010).

Since 1981, all zoos in the UK have been required to hold a licence under the ZLA. (See the section at the end of the chapter on **Websites and other resources** for details of online access to the full text of the ZLA; **Box 3.3** provides a brief overview of how zoo licensing works in practice in the UK.) The ZLA defines a zoo as a place where non-domesticated animals are kept and which is open to the public for at least seven days per year. It excludes pet shops (which are licensed under the Pet Animals Act 1951), circuses (which are covered by the Performing Animals (Regulation) Act 1925), and animals kept privately with no public access (exotic species listed as dangerous are licensed under the Dangerous Wild Animals Act 1976).[10]

Despite these exclusions, the scope of the ZLA is very broad and everything from large zoos to small aquariums and wildlife parks comes under its remit (**Plate 3.1**; see also **Box 3.3**). For example, an animal rescue centre with a few **exotic animals**, which is open to the public on just seven days a year, counts as a zoo in the eyes of the law.

As a result of the EC Zoos Directive, the ZLA was amended in 2002 to incorporate additional requirements relating to conservation and education. The full title of the legislation amending

---

[10] The Dangerous Wild Animals Act 1976 applies only to species listed as dangerous (see the Defra website at **http://www.defra.gov.uk**). Exotic species which are kept privately and are not listed as dangerous fall outside the scope of this Act, but do now come within the remit of the Animal Welfare Act 2006.

Box 3.3   HOW DOES ZOO LICENSING WORK IN THE UK?

The formal requirements for obtaining a licence for a new zoo are set out in the Zoo Licensing Act 1981 (Amendment) (England and Wales) Regulations 2002 (see **Websites and other resources**). There is a useful guidance document from Defra, published online in 2012, explaining the key points of the Zoo Licensing Act 1981 (ZLA), including how to go about applying for a zoo licence (see **http://www.defra.gov.uk**).

At least two months before a licence can be applied for, written notification of intent to open a new zoo must be given to the relevant local authority. This written notification must include a statement about how the zoo will implement the conservation measures detailed in the ZLA, as well as information about location, the kinds of animals that the zoo intends to keep, and various other details. A summary of this information must also be published in one local and one national newspaper, and displayed at the site of the proposed zoo. The local authority must then consider a zoo inspector's report before reaching a decision on whether or not to grant a licence for the new zoo. Once granted, a first licence runs for four years. Subsequent licences (usually renewal licences) run for six years.

For existing zoos, an application to renew a licence under the ZLA must be made at least six months before the expiry date of the old licence. Local authorities have the power to direct a zoo to apply for a new licence where they believe that there are good grounds for refusing a straightforward renewal. They also have the power, in exceptional cases, to require a zoo to close to the public for a period of time—or even to close permanently—if licence conditions have been breached.

Zoo inspectors are drawn from a list held by the Secretary of State. This list is in two parts: the first part contains names of veterinarians with experience of treating exotic animals; the second part lists persons judged to be competent (by the Secretary of State) to inspect zoos and to provide advice on keeping wild animals in captivity. The costs of a zoo inspection, which can take up to two full days, are usually paid in the first instance by the licensing authority, which then seeks reimbursement from the zoo.

---

the Act is the Zoo Licensing Act 1981 (Amendment) (England and Wales) Regulations 2002; this legislation came into force in the UK in January 2003. Because the ZLA was already in existence prior to the EC Zoos Directive, the consequent amendments to the Act took the form of secondary legislation, and so were not debated in Parliament. In fact, much of the content of the EC Zoos Directive was already built into the 1981 Act, notably those parts to do with maintaining standards of animal welfare. However, the EC Zoos Directive strengthened the requirement for UK zoos to build on those aspects of their work related to conservation. As a result, all zoos in the UK now have to demonstrate active involvement in conservation and/or research that furthers the aims of zoo conservation. They must also demonstrate

active involvement in educational programmes designed to raise public awareness and concern about conservation issues.

At first sight, these legal requirements for active involvement in conservation (**Fig. 3.6**) might appear onerous, particularly for small zoos with limited resources. However, they are in line with the stated aims and purposes of zoos, and guidelines and support are available to zoos (from organizations such as the Zoos Expert Committee in the UK, or BIAZA or EAZA or one of the other zoo associations—see **section 3.6.1**) on ways of interpreting and implementing these legal requirements.

Other aspects of the ZLA, as amended, include the requirement that zoos keep adequate records (see **Chapter 5**), prevent escapes, and maintain a safe environment for animals and humans (in
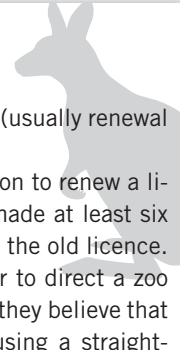
Figure 3.6 Reddish buff moth *Acosmetia caliginosa* enclosures at Paignton Zoo Environmental Park. This is a species native to the UK that is being bred in captivity as part of a conservation project run jointly with Natural England (formerly English Nature). Conservation initiatives, which can include education about conservation, are now a legal requirement for zoos in EU member states under the EU Zoos Directive of 1999. (Photograph: Paignton Zoo Environmental Park).

fact, much of the Act is about issues relating to health and safety in zoos). The Act also includes provision for the closure of zoos and the disposal of surplus animals. So the ZLA is more than just a vehicle for licensing zoos; it sets the operating framework within which zoos in the UK function.

As well as being the legislation under which licences to operate UK zoos can be granted, renewed, or withdrawn (see **Box 3.3**), the ZLA also includes a requirement for regular inspection of zoos. 'Regular' means once each year and inspection is the responsibility of the relevant local authority. During the six-year life of a zoo licence (for an existing zoo), two of the annual inspections should be Secretary of State inspections (Defra 2012a), as part of which local authority inspectors must be assisted and accompanied by one or more special zoo inspectors who are appointed by the Secretary of State (Kirkwood 2001b).

The purpose of licensing and inspection is to ensure that the zoo operates to required standards. Various guidelines are available to zoos to explain what these standards are, the most important of which are the Secretary of State's Standards of Modern Zoo Practice (SSSMZP) (Defra 2012a).

3.4.2 The Secretary of State's Standards of Modern Zoo Practice (SSSMZP)

Of course, responsible zoos do not need to be required by law to operate in the way specified by the various Acts and Directives already discussed in this chapter. But the fact that legislation such as the ZLA spells out what governments expect of zoos serves as a useful reminder to anyone involved in work with captive exotic animals of exactly what standards and goals they should be achieving. To help in the interpretation of the ZLA and other legislation, the UK government has produced guidelines on what the expected standards are for a wide variety of aspects of the zoo world. These guidelines are the Secretary of State's Standards of Modern Zoo Practice (Defra 2012a) and are regularly updated (the current version at time of writing is from 2012).

These guidelines are intended to set the standards that UK zoos are expected to achieve in all their work. Therefore the SSSMZP also function as an interpretation of the law and provide the criteria against which zoos' compliance with the law will be judged. The standards set out in the SSSMZP are based on the so-called

Figure 3.7 Part of routine husbandry at zoos is to ensure that animals have an appropriate, safe, and hygienic environment, which requires a considerable amount of time spent cleaning out enclosures. In the UK, this requirement is set out explicitly in government guidance for zoos, as a principle of animal care within the Secretary of State's Standards of Modern Zoo Practice (Defra 2012a). (Photograph: Christopher Stevens, Werribee Open Range Zoo)

five principles of animal care and management, which are themselves derived from the **five freedoms** that were originally applied in relation to the welfare of farm animals (FAWC 1992) (see **Chapter 7** on 'Animal welfare').

1. **Provision of food and water** This principle deals largely with the health and hygiene aspects of the provision of food and water, but also includes statements about the appropriateness of the quality, quantity, and variety of the food for the particular animal, taking into account features such as its species, sex, age, reproductive condition, and so on.

2. **Provision of a suitable environment** This principle includes statements about physical features of the captive environment and their appropriateness for the species being kept, as well as consideration of minimizing the possibility of animals escaping. Also included here are health and safety considerations (for example, electrical equipment servicing, broken

barriers) and aspects of hygiene (for example, rubbish disposal, cage cleaning— **Fig. 3.7**).

3. **Provision of animal health care** This principle is about the level of veterinary care provided for the animals (**Fig. 3.8**) and also about

Figure 3.8 This photograph shows a pre-release health check on a common or hazel dormouse *Muscardinus avellanarius*. This species is bred in captivity at a number of UK zoos, as part of captive breeding and reintroduction programmes. Participation in conservation activity is now a legal requirement for zoos in EU member states. (Photograph: Paignton Zoo Environmental Park).

disease prevention. It also includes reference to other kinds of health hazard, such as minimizing the likelihood of animals damaging each other. Finally, it reaffirms the need to keep comprehensive records of the animals and their health.

4. **Provision of opportunity to express most normal behaviour** This principle is to do with the provision of physical and social environments that promote behaviours similar to those seen in the wild. To do this, zoos are expected to be familiar with current knowledge of the behaviour of the animals in the wild. This part of the guidelines also makes statements about the importance of captive breeding and the avoidance of producing between-taxa hybrids.

5. **Provision of protection from fear and distress** Again, this includes statements about the provision of appropriate physical and social environments. It also includes reference to zoo visitors and the provision of facilities for animals to avoid human contact if they so choose.

These five principles constitute the main foundation of the standards set for animal care, but the SSSMZP also set standards for other aspects of zoo management, including:

- the transportation and movement of live animals;
- conservation and education measures;
- public safety in the zoo;
- stock records;
- staff and training;
- public facilities.

While not concerned primarily with animal care, these additional statements of standards are designed to inform zoos about what the UK government considers to be best practice in the operation of all aspects of the zoo organization. They are supplemented by a number of appendices, which help to interpret the EC Zoos Directive—notably, in terms of the requirement for zoos to be involved in conservation and education, but also in relation to animal transactions, veterinary facilities, animal contact areas, and the training of animals.

The SSSMZP also require zoos to confront and resolve ethical issues that may arise during zoo operation, through the establishment of a formal ethical review process.

3.4.3 Guidelines for best practice

In addition to the SSSMZP, zoos in the UK can find advisory guidelines on aspects of their work from sources such as the *Zoos Expert Committee Handbook* (Defra 2012b, available via the Defra website) and BIAZA.

The Zoos Expert Committee

The **Zoos Expert Committee** (ZEC) replaced the former **Zoos Forum** in February 2011. The Committee's main role is to provide independent technical advice to UK government ministers on matters relating to zoos, and particularly government policies on zoos. As part of this role, the Committee will advise on the operation of the zoo licensing system in the UK, and on the role that UK zoos can play in wildlife conservation.

The *Zoos Expert Committee Handbook* (Defra 2012b), which supplements the Secretary of State's Standards of Modern Zoo Practice or SSSMZP (Defra 2012a), was published online in November 2012, and replaces the *Zoos Forum Handbook* (Defra 2007b). The *ZEC Handbook* advises on how zoos can achieve the standards set out in the SSSMZP, as well as highlighting areas of good practice (**Fig. 3.9**).

At the time of writing, the *ZEC Handbook* included chapters on legislation; ethical review; conservation, education, and research; **sustainability** initiatives; veterinary services; and animal welfare and its assessment. Amongst the appendices to these chapters are real examples from real zoos, showing how policies on population management, disease prevention, and so forth have been set in place.
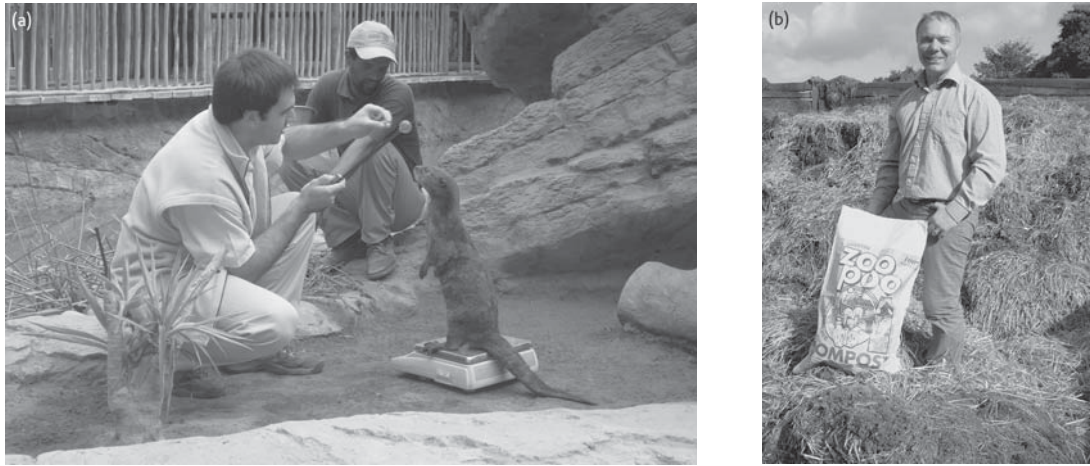
Figure 3.9 Some examples of best practice in how zoos look after animals and visitors, what they sell to visitors, and how they encourage environmental awareness: (a) training a spotted-neck otter *Lutra maculicollis* for weighing, as part of regular monitoring of body condition; (b) 'Zoo-Poo' for sale, to recycle zoo waste. (Photographs: (a) Cango Wildlife Ranch, South Africa; (b) Paignton Zoo Environmental Park)

BIAZA guidelines

The British and Irish Association of Zoos and Aquariums (BIAZA) is another body that provides guidelines and advice on best practice for UK zoos—as do other national and regional zoo associations such as the Association of Zoos and Aquariums (AZA) in North America, the European Association of Zoos and Aquariums (EAZA), and the Australasian Zoo and Aquarium Association or ZAA (formerly known as ARAZPA) (see **section 3.6**). BIAZA publishes animal management and **husbandry guidelines** on various species, and also codes of practice for member zoos on subjects as varied as animal transactions and the **euthanasia** of invertebrates. (Details of all of these publications can be found online at **http://www.biaza.org.uk**).

Other guidelines and sources of information for zoos

The Council for Learning Outside the Classroom is a UK charity which sets out its main aim as being to '*encourage young people to get out and about because research shows that children learn best through real world, hands on experiences*'. The Council took over responsibility for the Learning Outside the Classroom Manifesto (DfES 2006) in April 2009; this manifesto was originally drawn up by a UK government department, the former Department for Education and Skills (DfES).

The Association of British Wild Animal Keepers (ABWAK) is another source of information (see **http://abwak.org**), producing husbandry guidelines for a range of taxa.

3.4.4 Other UK legislation governing how zoos operate

In addition to the Zoo Licensing Act 1981, other legislation that impacts on zoos includes laws and regulations on areas as diverse as animal welfare, conservation, animal health and diseases, human health and safety (zoo staff and visitors), animal transport, employment, trade, building regulations, charity law and trust law, data protection law, waste disposal (animal by-products), and disability discrimination (Brooman and Legge 1997; Kirkwood 2001a) (**Fig. 3.10**). Even firearms legislation can apply to zoos (vets and keepers using darting equipment, or rifles for **pest** control, require a licence under the Firearms Acts

Figure 3.10 Zoos have to comply with a wide range of legislation, including, for example, disability discrimination legislation. Here, wheelchair users are watching the giraffes at Rotterdam Zoo. (Photograph: Geoff Hosey)

1968–1997). **Table 3.2** provides a summary of the main Acts other than the ZLA that govern the operation of UK zoos.

Government departments with some responsibility for aspects of zoos in the UK include Defra, the Department for Education, the Department for Business, Innovation, and Skills (BIS), the Home Office, and the Department of Culture, Media, and Sport (DCMS).

The Defra website contains comprehensive details of the legislation governing zoos in the UK.

Animal welfare legislation

The Animal Welfare Act 2006 (AWA) (which is criminal, rather than civil, law) came into effect in England and Wales in 2007. The equivalent legislation in Scotland is the Animal Health and Welfare Act 2006; in Northern Ireland, the relevant legislation is the Welfare of Animals Act (Northern Ireland) 1972.

The Act places a legal requirement (a 'duty of care') on the owners and keepers of animals (including zoo animals) not only to avoid cruelty, but also to ensure that the welfare needs of animals are met. These needs are summarized by Defra as follows:

- for a suitable environment (place to live);
- for a suitable diet;
- to exhibit normal behaviour patterns;
- to be housed with, or apart from, other animals (if applicable);
- to be protected from pain, injury, suffering, and disease.

The AWA covers all vertebrate animals, not just mammals, and also includes provision to extend its remit in the future to include non-vertebrate animals.

At the time of writing, there is also proposed new legislation in the UK to address the welfare of wild animals in circuses. After an initial consultation in 2012, it is likely that the UK government will seek to ban travelling circuses from using performing wild animals.

Topic	Act, Order, or Regulation	Further information
Animal health and disease	The Animal Health Act 2002	The 2002 Act deals with, among other things, government powers to tackle foot and mouth disease (FMD) and **transmissible spongiform encephalopathies (TSEs)** such as **BSE**.
	The Veterinary Medicines Regulations 2011	Most **analgesic drugs** for animals can only be prescribed by a vet who has seen and assessed the animal.
	The Misuse of Drugs (Amendment No. 2) (England, Wales and Scotland) Regulations 2012	These Regulations cover the use of opioids such as morphine.
Animal welfare	The Animal Welfare Act (England and Wales) 2006	The AWA 2006 brings together many existing pieces of animal welfare legislation for farmed and non-farmed animals.
	The Mutilations (Permitted Procedures) (England) (Amendment) Regulations 2008	These Regulations amend the 2007 Regulations of the same name, and allow some exemptions to the ban on the mutilation of animals set out in the AWA 2006. For example, the wing and web tagging of non-farmed birds for conservation purposes, including captive breeding programmes, is permitted under the Regulations.
	The Veterinary Surgeons Act 1966	
	The Animals (Scientific Procedures) Act 1986	This Act covers any invasive research on animals (such as research involving surgery) and may apply to some zoos in which veterinary or reproductive research is carried out. See **Box 3.4**
Building regulations	The Building Act 1984	
Conservation	The Wildlife and Countryside Act 1981	The WLCA implements European conservation regulations such as the Berne Convention (see online at **http://jncc.gov.uk/** for a useful guide to the WLCA).
Disability discrimination	The Disability Discrimination Act 1995	
Employment	The Data Protection Act 1998 The Employment Rights Act 1996	Zoos must keep records of the details of their employees, clients, and volunteers in accordance with the provisions of the DPA. This also applies to records of student trainees and researchers who may be working temporarily in the zoo.

Topic	Act, Order, or Regulation	Further information
Firearms	The Firearms Acts 1968–1997	Vets and keepers using darting equipment or other firearms must be licensed to do so.
General animal law	The Performing Animals (Regulation) Act 1925	This Act requires that people or organizations who train animals to perform in shows must register with their local authority and be subject to inspection.
General environmental protection law	The Environmental Protection Act 1990 The Control of Pollution (Amendment) Act 1989	
Health and safety	The Control of Substances Hazardous to Health Regulations 2002 (COSHH) The Health and Safety at Work Act 1974	The UK government Health and Safety Executive (HSE) has produced two useful online guides: *Managing Health and Safety in Zoos* (available at **http://hse.gov.uk/pubns/web15.pdf**), and a guide to the COSHH Regulations (available at **http://hse.gov.uk/pubns/indg136.pdf**).
Research	The Animals (Scientific Procedures) Act 1986 (A(SP)A)	See **Box 3.4** for further details about the A(SP)A.
Trade	The Control of Trade in Endangered Species (Enforcement) Regulations 1977 (COTES)	COTES is the domestic legislation in Britain implementing CITES (see **section 3.2.1** and **Fig. 3.1**).
Transport	The Welfare of Animals (Transport) (England) Order 2006	This Order replaces the older 1997 Order and brings national legislation into line with EU Council Regulation (EC) No. 1/2005 on the protection of animals during transport.
Waste management and disposal (including carcass disposal)	The Waste Management Licensing Regulations 1994 (as amended) *and* The Waste Management Licensing (Scotland) Regulations 2011 The Hazardous Waste (England and Wales) Regulations 2005	
	The Animal By-Products (Enforcement) (England) Regulations 2011	National legislation within the UK implements EU Regulation No. 1069/2009 and accompanying Implementing Regulation (EC) 142/2011 on the use of animal by-products; this legislation now allows zoos to carry out controlled 'feeding in' of animals.

Table 3.2 Other UK legislation affecting zoos

Note: This list is not exhaustive. In addition, legislation in Northern Ireland, Scotland, and Wales may differ (see **Box 3.2** for information about devolved legislation within the UK).

> **Box 3.4** **RESEARCH WORK REQUIRING A HOME OFFICE LICENCE**
>
> In the UK, the Animals (Scientific Procedures) Act 1986 covers any **invasive procedure**, described as '*any experimental or other scientific procedure applied to a protected animal … which may have the effect of causing that animal pain, suffering, distress or lasting harm*'. A protected animal, under the terms of the Act, is any living vertebrate (other than humans) and also one invertebrate species, the common octopus *Octopus vulgaris*.
>
> Before invasive research on a protected animal species can be carried out, there is a legal requirement under the Act to obtain a licence from the Home Office. This requirement might apply to a zoo if, for example, a normally **free-ranging** animal were to be caged temporarily, solely for the purposes of research. Even if a zoo research project is entirely observational, there is still a possibility that procedures such as the capture and/or confinement of animals can cause distress.
>
> The *ZEC Handbook* advises that zoos should seek guidance from the Home Office if there is any uncertainty over whether or not a particular research project requires a licence.

Legislation governing research in zoos

The Animals (Scientific Procedures) Act 1986 may on occasion apply to UK zoos in which research is being carried out, although Kirkwood (2001a) says that little, if any, zoo work is undertaken under this Act. **Box 3.4** provides further information about the Act and the sorts of circumstance under which zoos might be required to obtain a Home Office licence before undertaking research.

3.5 Zoo legislation outside Europe

There is insufficient space in this chapter (or indeed in this book) for a full account of legislation relating to zoos in all countries outside Europe. The following three sections provide a very brief overview of legislation governing zoos in North America, in Australia, and in the rest of the world, with details of where you can go to find further information.

3.5.1 Legislation governing zoos in the USA and Canada: an overview

In the USA, the Animal Welfare Act of 1966 (AWA) covers several aspects of zoo operations, from zoo licensing, to animal health, animal purchase, transportation, housing, handling, and husbandry (Vehrs 1996). It is the only federal legislation (as opposed to state legislation) in the USA that regulates the treatment of animals. Since its enactment in 1966, the AWA has been amended six times, most recently in 2008.

Responsibility for monitoring compliance with the AWA rests with the US Department of Agriculture's Animal and Plant Health Inspection Service (APHIS), which administers the granting of licences to zoological parks and aquariums via federal veterinarian services (each US state has a Veterinarian in Charge, whose responsibilities include overseeing licence applications by zoos). The AWA regulations apply only to mammals, and not to all species of mammal: farm animals, rats and mice, and most common companion animals are excluded from the provisions of the Act (Vehrs 1996). For marine organisms kept in captivity in the USA, only marine mammals have specific government regulations covering their environment; APHIS sets water quality standards for parameters such as salinity and pH.

Other US government agencies that are involved with the regulation of zoos are the Food and Drug Administration (FDA) and the US Fish and Wildlife Service (Department of the Interior); the latter enforces international legislation such as CITES. Fowler and Miller (1993), in the third edition of their comprehensive book

Zoo and Wild Animal Medicine, provide a list of US government departments and agencies, together with a summary of current zoo-related legislation (this useful summary is not included in every edition).

Grech (2004) offers a useful (online) review; the website of the Association of Zoos and Aquariums (AZA) also provides information about federal laws that impact on the operation of zoos, and has links to other websites, including that of the Code of Federal Regulations. Gesualdi (2001) looks at zoo licensing and accreditation in Canada and in Mexico, as well as in the USA.

It is worth noting that zoo legislation in Canada varies markedly from one province to another. Ontario, in particular, has come in for criticism in recent years for a lack of adequate legislation covering small 'roadside' zoos (Dalgetty 2007).

3.5.2 Legislation governing zoos in Australia

As in the USA and Canada, Australia has both national and state (or territory) legislation. The law relating to zoo animals in Australia varies quite widely between the six states and two territories, although some national issues are dealt with by the Commonwealth government (this includes quarantine, and also compliance with international treaties such as CITES). However, most day-to-day governance of zoos is at state or territory level. Taking just three of the states as examples, in Queensland zoo regulation falls under the Nature Conservation Regulation 1994, and also under other legislation such as the Queensland Animal Care and Protection Act 2001. In New South Wales, key legislation governing zoos includes the Exhibited Animals Act Regulation 1995. Finally, the State of Victoria has legislation which specifically refers to zoos, namely the Zoological Parks and Gardens Act 1995.

The ZAA has a Legislation and Standards Review Working Group (see the ZAA website for details), which provides guidance to zoos in Australasia on legislative matters.

3.5.3 Legislation governing zoos outside North America, Australia, and Europe: an overview

The website of the Zoo Outreach Organisation (ZOO) (**http://zooreach.org**) provides much useful information about zoo legislation, standards, and guidelines for zoos in South Asia and Southeast Asia (**Fig. 3.11**) (and indeed also zoos in Australia). There is wide variation among countries in this region between their approaches to zoo legislation and, in particular, whether the

Figure 3.11   There is wide variation between countries in Southeast Asia in the regulatory framework governing how zoos operate. These photographs are from two leading zoos in the region, and show (a) a capybara *Hydrochaerus hydrochaeris* at Singapore Zoo and (b) the entrance to the Schmutzer Primate Center at Ragunan Zoo, Indonesia. (Photographs: (a) Diana Marlena, Singapore Zoo; (b) Vicky Melfi)

regulation of zoos is managed predominantly nationally or locally. In India, for example, there is both specific legislation and a zoo licensing system that recognizes four different categories of zoo, according to the size of the zoo; there are different regulatory requirements for each category (Cooper 2003). Zoo regulation in India is set out in a comprehensive guide, available as a book, under the title *Zoos in India: Legislation, Policy, Guidelines and Strategies* (Central Zoo Authority 2009); this is updated at regular intervals.

Elsewhere in Asia, the picture is very mixed. Like India, Sri Lanka has specific zoo legislation. Several other countries, including Malaysia, Singapore, and Japan (**Plate 3.2**) have wildlife protection legislation which covers some aspects of zoo management. In China, there is legislation to protect endangered species in the wild (the Law of the People's Republic of China on the Protection of Wildlife 1988) but as yet there are no animal welfare laws or other legislation to protect wild animals in captivity. In March 2011, draft animal protection legislation was presented to the Chinese government during the annual National People's Congress. This proposed new legislation has widespread public support, but at the time of writing there is no clear timetable for its adoption.

For information about legislation governing zoos in Africa or South America, the best starting point is the website of the zoo association for the region. These are, respectively, the African Association of Zoological Gardens and Aquaria (PAAZAB) and the Latin-American Zoo and Aquarium Association (ALPZA). There is more about zoo associations in the next section of this chapter.

3.6 Zoo associations: from BIAZA and EAZA, to AZA, ZAA, and WAZA

Most zoos do not operate in isolation, but belong to zoo associations at a national or regional level (**Fig. 3.12**). These associations are not generally part of the legislative framework within which zoos operate, but they can be thought of as part of the regulatory framework, because part of their purpose is to promote professionalism and good practice within the zoo world, and to help to administer—at an inter-organizational level—the conservation, research, and educational functions of zoos.

The oldest national zoo association is the German Association of Zoo Directors (*Verband Deutscher Zoodirektoren*), founded in 1887; this gave birth to the International Union of Directors of Zoological Gardens (IUDZG) in 1935 at a meeting in Basel (EAZA 2003). Today, the emphasis is on zoo associations, rather than on zoo director associations, although there are also thriving zookeeper organizations in many countries.

3.6.1 The British and Irish Association of Zoos and Aquariums (BIAZA)

Zoos in Great Britain and Ireland are encouraged to become members of BIAZA, which sees itself as the professional organization representing the zoo and aquarium community. BIAZA was founded in 1966 and was formerly known as the Federation of Zoos of Great Britain and Ireland.

Zoos and aquariums can become full members of BIAZA, but there are also several categories of associate membership available for companies operating within the zoo world, for educational establishments such as universities that have links with zoos, and for individuals. BIAZA organizes meetings, including an annual research symposium; it also publishes guidelines, promotes research, and manages conservation work. The aims of BIAZA are to promote conservation and public concern for the natural world, and to achieve high standards of animal care in the zoo community. (See **section 2.5.1** for more on the published mission and vision of BIAZA.)

BIAZA also produces much useful advice on legislation governing zoos. This is available via the

Figure 3.12 Accredited zoos are zoos that are licensed and which belong to zoo associations at national or regional levels. (Logos courtesy of BIAZA, EAZA, WAZA, and ZAA)

BIAZA website and also in 'Legal Lines', a short section in each edition of *Lifelines*, BIAZA's quarterly magazine.

3.6.2 The European Association of Zoos and Aquaria (EAZA)

Many British zoos are also members of EAZA. Set up in 1988 to represent zoos in the EU, EAZA was originally known as the European Community Association of Zoos and Aquaria (ECAZA). With the fall of the Iron Curtain, the organization was able to expand eastwards and, today, EAZA has members in countries both within and bordering Europe, including Israel, Turkey, and, as of early 2007, Cyprus. Further afield, zoos in Kuwait, Qatar, and Kazakhstan are associate members of EAZA.

EAZA now has (at the time of writing) 345 member zoos spanning forty-one countries, with its main executive offices in the grounds of Artis Zoo in Amsterdam. EAZA's mission comprises four strands: planning and coordinating wildlife conservation through the region; promoting education, particularly about the environment; contributing to discussion at an international level

(for example, among the United Nations, EU, etc.); and advising the European Union and its committees. EAZA places a strong emphasis on captive breeding and involvement in regional **captive management programmes**, reflecting its origins in the creation, in 1985, of the first **European Endangered species Programmes (EEPs)**.[11]

To become EAZA members, zoos and aquariums must undergo a rigorous accreditation process. Member zoos must maintain details of their collection on a computer system using the Animal Record-Keeping System (ARKS), or the more recent web-based Zoological Information Management System (ZIMS) when available (see **Chapter 5**). EAZA also requires collection data to be included on the global zoo animal database of the International Species Information System (ISIS; see **http://isis.org**), allowing information to be retrieved quickly.

EAZA members must also comply with EAZA's standards and code of **ethics**. EAZA has produced a number of policy documents and sets of standards by which member zoos are to operate, and was instrumental in formulating the EC Zoos Directive.

3.6.3 The Zoo and Aquarium Association (formerly ARAZPA)

The ZAA, established in 1990 as the Australasian Regional Association of Zoological Parks and Aquaria, or ARAZPA, links more than eighty zoos and aquariums across Australia, New Zealand, and the South Pacific.

3.6.4 The Association of Zoos and Aquariums (AZA)

With more than 6,000 members today, the US-based AZA claims to be the largest zoo and aquarium association in the world. However, fewer than 250 of this total are accredited zoo members of the AZA; others are individual members. Membership of the AZA is now also open to individuals and zoos from outside North America; a zoo in Mexico and another in Hong Kong are among the accredited members.

Founded in 1924 as the American Association of Zoological Parks and Aquariums (AAZPA), the organization changed its name to the American Zoo and Aquarium Association in 1994 and, at the same time, adopted the simple 'AZA' acronym. Today, the Association has dropped the 'American' and refers to itself simply as the Association of Zoos and Aquariums.

AZA has a variety of membership categories for zoos, other organizations, and individuals, and is worldwide in scope. Its mission is to promote excellence in animal care and welfare, conservation, education, and research, and to encourage respect for the natural world. Like BIAZA and EAZA, AZA publishes policies, guidelines, and codes of practice that are intended to support the work of members and to promote professional high standards.

3.6.5 The World Association of Zoos and Aquariums (WAZA)

Originally the International Union of Directors of Zoological Gardens (IUDZG), this association was renamed the World Association of Zoos and Aquariums (WAZA) in 2000. Membership is open to individual zoos and aquariums (which must, however, already also belong to a regional association), to the various regional and national associations, and to related organizations such as the International Species Information System (ISIS), the Institute for Zoo and Wildlife Research (IZW), and the like.

WAZA states as its mission '*WAZA is the voice of a worldwide community of zoos and aquariums and catalyst for their joint conservation action*' (WAZA 2012).

---

[11] European Endangered species Programmes are known as EEPs, not as EESPs, because the acronym is taken from the German, *Europäisches Erhaltungszuchtprogramm*.

One of WAZA's best-known achievements has been the production of three important strategy documents relating to wildlife conservation work by zoos. The first of these, the World Zoo Conservation Strategy (WZCS) (IUDZG/CBSG 1993), was published jointly in 1993 by the IUCN's Captive Breeding Specialist Group (CBSG) and WAZA in its former guise of the IUDZG. The second strategy document is the World Zoo and Aquarium Conservation Strategy (WZACS) (WAZA 2005). The third document, published in 2009, is entitled '*Turning the Tide: A Global Aquarium Strategy for Conservation and Sustainability*' (WAZA 2009). Each of these strategy documents is discussed in more detail in **Chapter 10** on 'Conservation'.

WAZA has also developed a Code of Ethics (WAZA 1999), which deals with issues ranging from contraception and euthanasia to the movement of animals between zoos.

Figure 3.13 A keeper at Pretoria Zoo, South Africa, carrying food the traditional way. In Africa, the zoo association is the African Association of Zoological Gardens and Aquaria (PAAZAB). (Photograph: Robyn Ingle-Jones, Pretoria Zoo)

3.6.6 Other zoo associations

National and regional zoo associations

Other areas of the world also have zoo associations that operate in much the same way and with the same sorts of values as those described above. These include, among others:

- the African Association of Zoological Gardens and Aquaria (PAAZAB)—formerly the Pan-African Association of Zoological Gardens and Aquaria, which is why there is still a P at the start of the acronym (**Fig. 3.13**);
- the Latin-American Zoo and Aquarium Association (ALPZA);
- the Canadian Association of Zoos and Aquariums (CAZA);
- the South-Asian Zoo Association for Regional Cooperation (SAZARC).

Keeper associations

As well as zoo associations, there are various zookeeper associations worldwide. In the UK, the Association of British Wild Animal Keepers (ABWAK) produces its own magazine, *Ratel*, and other publications such as husbandry guidelines for a number of taxa. ABWAK also offers small grants for work in zoos.

The ABWAK website (**http://abwak.org**) provides further information and contact details (and is also a good place to start if you are looking for a job as a keeper in a British zoo).

The American Association of Zoo Keepers (AAZK) fulfils a similar role in North America. Among the publications produced by AAZK is its *Enrichment Notebook* (2004), now in its third edition and available as a searchable CD-ROM (see **http://aazk.org** for further details). AAZK also produces a CD-ROM on *Zoonotic Diseases*, with a searchable list of **zoonoses** and a useful section on disinfection and hygiene (AAZK 2008).

In Australia and New Zealand, there is the Australasian Society of Zoo Keeping (ASZK); Africa has the Animal Keepers Association of Africa (AKAA). In Europe, there are various organizations, such as the European Elephant Keeper and Manager Association (EEKMA), as well as national zookeepers' associations.

In 2000, at a meeting in Columbus, Ohio, the idea of an International Congress on Zoo-keeping (ICZ) was born, and the first was held in 2003 at Avifauna, at Alphen aan den Rijn in the Netherlands. This was followed by a second meeting of the ICZ in Australia in 2006, with Seattle the venue for 2009, and Singapore in 2012. The ICZ website (**http://iczoo.org**) lists the main national and regional zookeepers' associations worldwide.

Summary

• Zoos are governed by a wide and complex range of legislation, and non-legislative agreements and guidelines, operating at international, national, and sub-national levels.

• Not all countries have specific 'zoo' legislation. In the USA, for example, the main legislation within which zoos must operate is the Animal Welfare Act of 1966.

• Zoos in the UK are regulated by the Zoo Licensing Act 1981 (ZLA), as amended, which incorporates into UK law the requirements of the 1999 EC Zoos Directive (1999/22/EC).

• The ZLA and the EC Zoos Directive lay requirements on zoos to fulfil certain obligations in order to be allowed (licensed) to operate.

• Zoos in EU countries must now be engaged actively in both education and conservation to meet the requirements of the EC Zoos Directive.

• Help for UK zoos in understanding their legal obligations and achieving best practice is available in government guidelines—the Secretary of State's Standards of Modern Zoo Practice (SSSMZP) (Defra 2012a)

• Regional, national, and international zoo associations such as BIAZA, EAZA, ZAA, AZA, and WAZA also aim to promote best practice and to coordinate the activities of zoos.

Questions and topics for discussion

1. Is the definition of a 'zoo' within the UK, as set out in the Zoo Licensing Act 1981, too broad to be useful?

2. Should membership of a national or regional association such as BIAZA, EAZA, AZA, or ZAA remain voluntary, or should it be made compulsory for all zoos as a condition of licensing?

3. Should all zoos be required, by law, to participate in conservation and education initiatives, or should some smaller zoos be exempt from this requirement?

4. In addition to the Zoo Licensing Act 1981, as amended, what other legislation governs how zoos operate within the UK?

5. Compare and contrast the legislative framework for zoos in the USA, Australia, and Europe.

Further reading

For those who want to delve more deeply into the complex regulatory framework within which zoos operate, a good starting point is Chapter 3, 'Importance and application of animal law', in Cooper and Cooper's *Introduction to Veterinary and Comparative Forensic Medicine* (2007). It is also worth reading Chapter 4, 'Animal welfare', in the same book. Margaret Cooper (a lawyer who specializes in animal law) has written a very helpful summary paper on zoo legislation for the *International Zoo Yearbook* (2003). This contains, as an appendix, a table of examples of zoo legislation for various countries around the world. More recently, Barber *et al.* (2012) have provided a good overview of accreditation and the regulatory framework for zoos in North America, Southeast Asia, and Europe.

For further reading about animal welfare law in Britain, we recommend Mike Radford's *Animal Welfare Law in Britain: Regulation and Responsibility*

(2001). We also recommend Brooman and Legge's *Law Relating to Animals* (1997). This features a section on legislation relating to zoos (as well as a short summary of zoo history). Although published in the UK, the book considers European and international law relating to animals, and also covers animal welfare legislation in Australia.

Within the three volumes of the *Encyclopedia of the World's Zoos* (Bell 2001), there are several entries about zoo legislation and licensing processes. James Kirkwood (formerly Chief Veterinarian at ZSL and now the Director of the Universities Federation for Animal Welfare) has contributed two useful summaries covering UK zoo legislation and licensing processes (Kirkwood 2001a; 2001b). Other entries include an overview of legislation and licensing for zoos in Africa (Walker 2001), and licensing and accreditation for zoos in North America (Gesualdi 2001).

Websites and other resources

We have found the following websites and other sources of information to be particularly useful, although there are occasional inaccuracies in some of the published website addresses and online information, and we would always recommend that readers double-check against another source. The full text of some of the key documents referred to in this chapter can be downloaded from the following websites.

- **The Convention on Biological Diversity (CBD)** The text of the Convention is available online at **http://cbd.int/convention/convention.shtml**
- **The EC Zoos Directive (1999/22/EC)** The full text of the EC Zoos Directive is available online at **http://europa.eu/legislation_summaries/environment/nature_and_biodiversity/l28069_en.htm**
- **The Zoo Licensing Act 1981, as amended, and the Zoo Licensing Act 1981 (Amendment) (England and Wales) Regulations 2002** The full version of the Regulations amending the Zoo Licensing Act 1981 (© Crown Copyright 2002) is available online at **http://legislation.gov.uk** A useful summary of the key points of the Zoo Licensing Act 1981, as amended, is available from Defra

('*Zoo Licensing Act 1981: Guide to the Act's Provisions*') at **http://defra.gov.uk**
- **The Secretary of State's Standards of Modern Zoo Practice (SSSMZP)** The SSSMZP (Defra 2012a) can be found online at **http://defra.gov.uk/publications/files/standards-of-zoo-practice.pdf**

The legislative framework for zoo licensing in the UK is operated through Defra, and a great deal of information is available from the Defra website (**http://defra.gov.uk**). Information about the Zoos Expert Committee, including details of meetings and publications, and copies of the *Zoos Expert Committee Handbook* (Defra 2012b) can be obtained from the same address and website.

The Scottish Government website (**http://scotland.gov.uk**) is a good source of information about devolved legislation, such as animal welfare legislation, in Scotland; the corresponding websites for Northern Ireland and for Wales are **http://northernireland.gov.uk** and **http://wales.gov.uk**

Information about BIAZA, the work it does, and its meetings can be obtained online at **http://biaza.org.uk**. Similarly, information about EAZA and its work can be found at **http://eaza.net**. The website address for AZA is **http://aza.org**. For ZAA, the details are **http://www.zooaquarium.org.au**, and for WAZA they are **http://waza.org**. If the zoo association which you are interested in is not listed here, the *Encyclopedia of the World's Zoos* (Bell 2001) contains entries for all the major zoo organizations throughout the world; there are also links from the WAZA website to other zoo organizations.

TRAFFIC (a joint programme of WWF and the IUCN) has produced a very helpful summary of the documentation needed for trading wild animals (and animal specimens) into and within the EU. This can be found at **http://eu-wildlifetrade.org**, although there are plans to move this information to the EU's CITES webpages in the near future. The implementation of the Convention on Biological Diversity (CBD) within the EU is summarized in an EC publication, *The Convention on Biological Diversity: Implementation in the European Union*. This is available online at **http://ec.europa.eu/environment/biodiversity/international/pdf/brochure_en.pdf**

The Eurogroup for Animal Welfare provides access to a useful publication that monitors the implementation of the EC Zoos Directive in member states, the *Report on the Implementation of the EU Zoos Directive* (Eurogroup for Animal Welfare 2006), which is available online at: **http://eurogroupforanimals.org/files/policies/downloads/66/reportzoos1208.pdf**

For information about legislation governing zoos in South East Asia, the Zoo Outreach Organisation publishes much useful information online at **http://zooreach.org**

Finally, for zoos within the UK, an excellent explanation of the Wildlife and Countryside Act 1981 (WLCA) is available online through the Joint Nature Conservation Committee (JNCC) at **http://jncc.gov.uk/page-3614**

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.

http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Chapter 4

Behaviour

The study of behaviour[1] is about understanding what animals do and why they do it. It is about the way in which animals acquire resources (such as food, shelter, or mates) and avoid danger (such as predators or **agonistic behaviours** among competitors), so understanding behaviour is crucial to our understanding of the animal's **life history traits** and its interactions with its environment. How an animal behaves can also help us to interpret its health and welfare, so observing behaviour is an important part of the captive management of **zoo** animals.

For many years, research on animal behaviour was dominated by studies of **learning** and, even then, the importance of the research was primarily seen as what it could tell us about human learning. But in the last 40 or 50 years, there has been a huge growth in studies of animal behaviour from an evolutionary viewpoint, and the emphasis now is on understanding how behaviour helps the animal to survive in its natural environment. We now have a substantial body of theory and experimental evidence to guide our understanding of animal behaviour.

In this book, we do not have the space to do any more than briefly summarize this theoretical background in a way that we hope makes the rest of the chapter intelligible, but we would urge anyone interested in finding out more to read one of the many excellent textbooks on animal behaviour that are currently available (see **Further reading** at the end of the chapter). Our main aim in this chapter is to examine the ways in which living in a zoo can affect the behaviour of the animals, and how we should interpret these changes. This then leads on to more applied uses of our behavioural knowledge in interpreting welfare (**Chapter 7**) and modifying the behaviour of the animals (**Chapter 8**, on **enrichment**, and **Chapter 13**, on 'People in zoos').

We will cover the following topics in this chapter.

- **4.1**　**General principles**
- **4.2**　**Animal behaviour in the zoo**
- **4.3**　**Behavioural responses to the zoo environment**
- **4.4**　**Abnormal behaviours**
- **4.5**　**Comparison with the wild**

In addition, some of the issues raised will be explored further, with specific examples, in boxes.

---

[1]　Animal behaviour involves a number of sub-disciplines, so you may also encounter terms such as 'ethology' (which broadly refers to the study of an animal's natural behaviours), 'comparative psychology' (which is mostly, but not totally, about animal learning), and 'behavioural ecology' (which is about how behaviour helps animals to survive). These terms are used to represent different traditions and theoretical approaches, but nowadays the distinctions between them are very blurred.

4.1 General principles

At the most basic level of explanation, behaviour can be described in terms of the **responses** animals make to **stimuli** in their environment; stimuli may be aspects of the physical environment (for example, light, temperature, sound) or may come from other animals (for example, signals such as chemicals, postures, calls). At a more complex level of explanation, we must recognize that animals may initiate some behaviours in the apparent absence of identifiable stimuli and that behaviour may be guided by internal (also called endogenous; for example, motivational—see **section 4.1.3**) as much as by external (exogenous) factors.

Like other aspects of an animal's biology, much behaviour is adaptive—that is, it evolves over generations by the process of natural selection, changing animals so that they are better able to survive and reproduce in their environments. For this to happen, variability in the animals' behaviour must reflect variability in their genes (or, in other words, behavioural differences between individuals must have a genetic basis), because any other differences—such as those arising from an animal's learning—that do not have a genetic basis will not evolve. Thus behaviour can alter between generations through genetic processes, leading to the evolution of new or modified forms of behaviour that increase the animal's **fitness**.

But behaviour differs from many biological processes in that it is often very flexible, to the extent that it can change dramatically within the lifetime of the individual. Behaviour that changes within the lifetime of the individual is usually the result not of genetics, but of experience—a process referred to as learning. Such behavioural change is not usually transmitted to subsequent generations, although it can be under the special conditions of social learning (see **section 4.1.2**).

Very often the questions we ask about animal behaviour are to do with what the purpose of the behaviour is and why the animal has evolved to do it this way rather than another way. These are often referred to as **functional** (or **ultimate**) explanations. But our explanation of behaviour can also be about why an animal is behaving in a particular way at that particular time. The answers to this sort of question—usually referred to as **causal** (or **proximate**) explanations—often require a recognition of which stimuli the animal is responding to, as well as other features, such as genetic differences, hormones, and levels of motivation, which can influence the likelihood and extent of the response. A useful way of deciding what sort of question we are asking is to use Tinbergen's 'Four Whys' (see **Box 4.1**). Note that the first 'why' requires a functional answer, whereas the other three are predominantly causal.

4.1.1 Behavioural repertoires

We have just stated that behaviour evolves if it has a genetic basis. But what do we mean by 'genetic basis'? Genes are variable stretches of a substance called deoxyribonucleic acid (DNA) and they provide the instructions for building proteins. So to say that genes 'produce' behaviour is nonsense. But the proteins for which genes code may be involved in the formation and operation of the nervous system, or may be hormones and other chemicals that initiate or maintain physiological states. Thus, genes can influence behaviour through a number of complex pathways and systems. But whatever the **genotype** of the animal, its behavioural **phenotype** is probably always the end result of those pathways and systems interacting with the environment in which the animal lives. The extent of that interaction varies according to things such as the function of the behaviour, the life history of the animal, and the complexity of the environment in which the animal lives.

Animals, then, have a repertoire of behaviours that is based on genetically mediated behaviours, which are the product of evolution; the expression of these behaviours is then modified to different extents by learning—the product of the animal's experience of its environment. It should be possible to compile a catalogue (an **ethogram**) of all of the kinds of behaviours seen in animals of a particular species. Such ethograms have, indeed, been published for several species, and even incomplete ethograms (which only catalogue the

Box 4.1 TINBERGEN'S 'FOUR WHYS'

Our interest in animal behaviour generally revolves around trying to understand why an animal behaves in a particular way that we have observed. In this context, the question 'why?' can mean several different things and therefore we can arrive at several different answers. Niko Tinbergen, one of the founders of modern ethology, recognized this and identified four different 'whys' that give us different perspectives on animal behaviour; these still form the framework for behavioural research (Tinbergen 1963).

Thus, our 'why' can be asking any one of the following.

1. **What is the function of the behaviour?** This is asking about how the behaviour affects the fitness of the animal—that is, how it allows the animal to survive and reproduce in its natural environment.

2. **What is the cause of the behaviour?** This is asking what are the immediate influences that lead to the animal showing that behaviour at that particular time. These might be internal or external stimuli or states.

3. **What is the course of development (**or ontogeny**) of the behaviour?** This is asking about the stages in the life history of the individual at which the particular behaviour may be shown and what influences the way in which the behaviour might change as the individual matures.

4. **How did the behaviour evolve?** This is asking about the evolutionary history of the behaviour—that is, how the behaviour has come to be the way it is. Of course, behaviour is rarely captured in the fossil record, so inferences about evolution are usually made comparatively—that is, by looking across closely, and more distantly, related species.

Suppose, for example, we see a small **Carnivore**[2] such as a genet *Genetta genetta* doing a handstand, as in **Fig. 4.1**. What is it doing?

Applying Tinbergen's four whys allows us to understand the behaviour better. In response to 'Why' (1), we find that its function is to apply a scent mark from perineal glands to a substrate; genets use this to recognize individuals and to find out something about their physiological state (Roeder 1980). In response to question (2), we will identify that a number of stimuli may cause scent marking; for example, anogenital scent marking in the genet may increase in males, but decrease in females, during periods of aggression (Roeder 1983). In relation to question (3), frequencies of scent marking are low in young genets, but increase as they get older (Roeder 1984). Finally, in relation to question (4), we find that the handstand position is used for anogenital scent marking in several other viverrid species as well (for example, the dwarf mongoose *Helogale parvula* and the kusimanse *Crossarchus obscurus*), but not in others (for example, the banded mongoose *Mungos mungo* uses anal dragging) (Ewer 1968), which might allow us to find life history correlates (for example, the need to raise the mark above ground level) to explain why the genet does its marking by handstand rather than any other way.

Figure 4.1 Genet performing an anogenital scent mark using a handstand position. (Photograph: Geoff Hosey)

---

[2] A **Carnivore** (with an initial capital C) is a member of the mammalian order Carnivora, which includes canids such as the foxes and wolves, felids such as lions and tigers, and other animals such as bears. A carnivore (with an initial lower-case c) is an animal that eats the flesh of other animals. So sharks and snakes are carnivores, but not Carnivores, whereas a hyaena is both.

Behaviour	Description
Scent marking	Males and females scent mark in different ways. Males perform an anal drag, moving forward (usually over bare earth or female faeces). Females perform an anal rock, remaining *in situ*.
Refection	Maras practise refection (the ingestion of their own faeces) infrequently and not as a regular daily habit as in the lagomorphs. The reingested faecal pellets are apparently no different in texture or size from normally excreted pellets. Refection involves a head-to-anus movement, often difficult to distinguish from penis licking in males.
Threat	Invariably a male–male behaviour, threat describes an animal facing a conspecific, with its head tilted backwards and mouth open to expose the teeth.
Chase	Chase describes a fast aggressive run towards another animal, often accompanied by threat behaviour.

Table 4.1 Extract from an ethogram for the mara *Dolichotis patagonum**
*From Pankhurst (1998).

most frequently seen behaviours, or a particular class of behaviours) are usually the necessary starting point for a behavioural investigation.

An example of part of an ethogram for the mara *Dolichotis patagonum* is shown in **Table 4.1**. Note that each behavioural unit is described in such a way that other observers could also use the ethogram and be confident that they were correctly identifying the behaviours. Often, ethograms are supported by photographs or drawings showing what the behaviours look like. We have included several here for the mara (**Fig. 4.2**), and you can see that they help greatly in describing the behaviours that you are likely to see this animal performing.

The animal's full repertoire of behaviours can be thought of as **species-typical behaviours**, meaning that they characterize the way in which members of that species behave in the wild. The extent to which animals in zoos show species-typical behaviours depends on the opportunities afforded by the physical and social aspects of their environment. For example, prey catching by predatory animals may not be possible in most zoo environments. Nevertheless, **behavioural diversity** (that is, a wide range of different behaviours) is seen as a good measure of how closely the zoo environment allows animals to display species-typical behaviours and is thus relevant to their welfare.

4.1.2 Learning

Learning can be thought of as the process that takes place when an experience of some sort brings about a relatively permanent change in the way in which an animal responds to a situation (Pearce 2008). Traditionally, theorists have identified several apparently qualitatively different kinds of learning, although it is possible that these may be more similar than was previously thought. The major kinds are:

- **habituation**, in which the animal reduces its response to a constant or repetitive stimulus;

- **classical conditioning** (also known as **Pavlovian conditioning**),[3] in which the animal learns to associate an existing response with a new stimulus (for example, showing food-related behaviours not to food itself, but to the sound of it being prepared);

- **operant conditioning**[4] (also known as **instrumental conditioning**), in which the animal

[3] 'Pavlovian' refers to the Russian physiologist Ivan Pavlov (1849–1936), who famously trained dogs to salivate to the sound of a metronome, anticipating that it signalled the delivery of food.

[4] Called **operant** because the animal's responses operate on (i.e. affect) the environment, which is why the animal learns them.
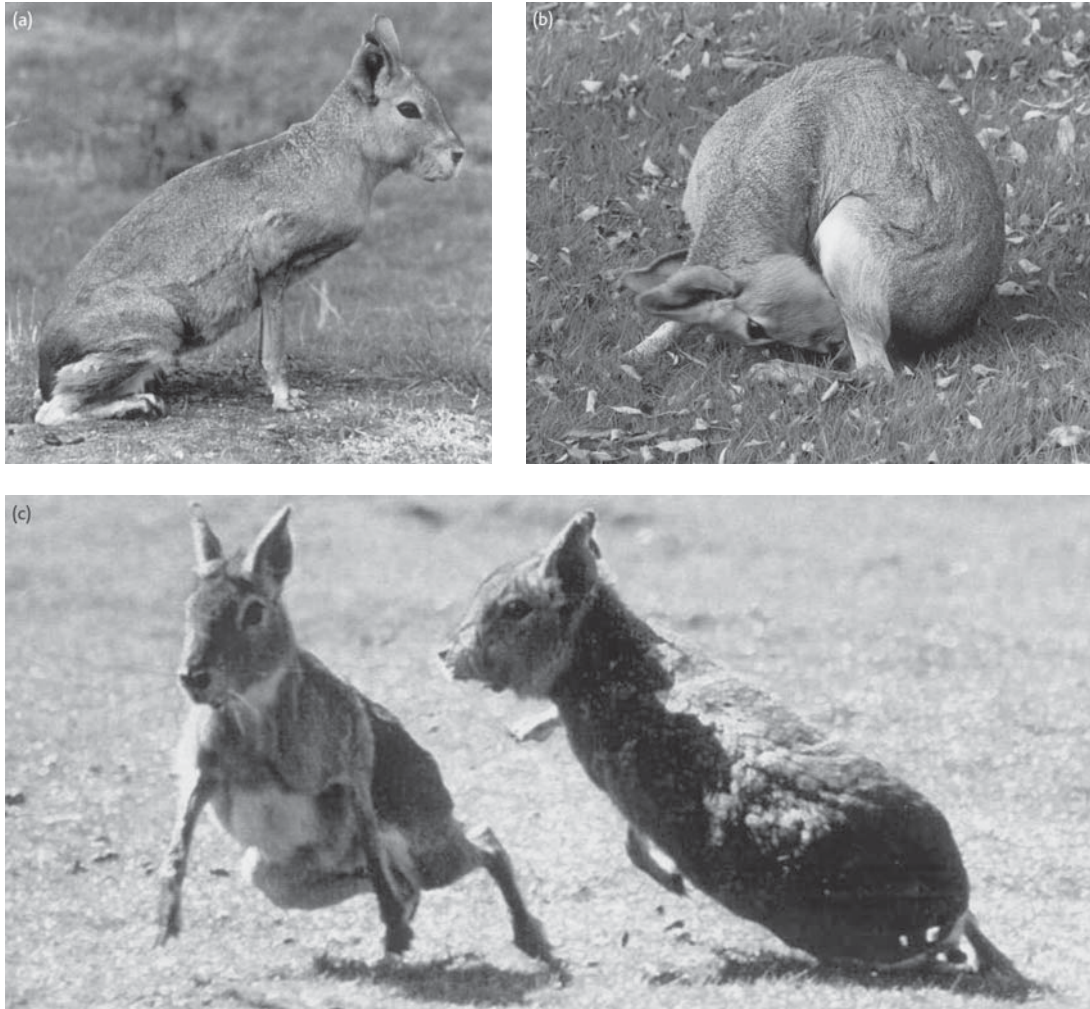
Figure 4.2 (a) Scent marking, (b) refection, and (c) aggressive chase in the mara *Dolichotis patagonum*. Pictures such as these help observers to use the written descriptions in the ethogram. (Photographs: Sheila Pankhurst, from Pankhurst 1998)

acquires a new response to an existing stimulus (for example, pressing a lever in order to get food);

• **imprinting**, in which young animals learn about their species identity, sex identity, or relatedness to other individuals.

The significance of learning in animals is that it permits them to detect patterns and relationships between objects and events in their environment. An important aspect of this is associative learning, in which animals learn which events reliably signal consequences that are important for them, and which can be achieved through both classical and operant conditioning. Animals also learn the differences between things (discrimination learning), and there is increasing evidence of their ability to learn routes, topography, categories, numerical quantities, and a variety of other things, often collectively referred to as complex learning, because they require more than only the formation of associations (Atkinson *et al.* 1996).

It is worthwhile looking a bit more closely at associative learning, because it underpins much of the way that animal behaviour is managed in zoos.
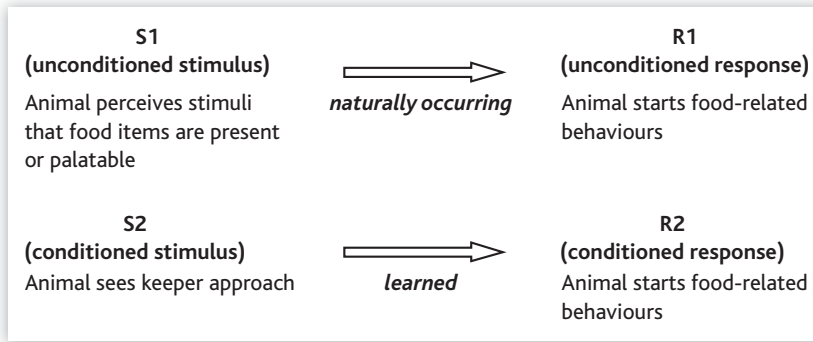
Figure 4.3 Simplified diagram to show the process of classical conditioning. The animal responds naturally to olfactory, visual, and other stimuli from food by showing food-related behaviours, such as salivation, sniffing, etc. In time, the animal may learn that the approach of the keeper is a reliable signal that food will follow, so it sets up an association between S1 and S2. Subsequently, the animal shows responses of food-related behaviours to the keeper's approach (R2), which are very similar to those it naturally shows to the presence of food (R1).

Associative learning

Associative learning occurs when there is a change in the animal's behaviour as a consequence of one event being paired with another (Pearce 2008). Exactly what events are being paired depends, to some extent, on the kind of learning that is taking place, but commonly two stimuli are paired (classical conditioning) or a stimulus is paired with a response (operant conditioning).

In classical conditioning, a neutral stimulus,[5] known as the 'conditioned stimulus' (CS), is paired with the natural biologically relevant stimulus, or 'unconditioned stimulus' (US), to produce a response—the 'conditioned response' (CR)—that, in most cases, is very similar to the ordinary response—or unconditioned response (UR)—to the biologically relevant stimulus. The CS–US association tells the animal about events in its environment; the CS is a sign that the US is coming.

In the zoo setting, animals learn these sorts of associations all the time (Young and Cipreste 2004). The appearance of a familiar keeper, activity in the food preparation room, members of the public starting to appear, and all sorts of other events signal to the animal that something else is likely to happen. Classical conditioning is also a part of husbandry training animals—for example,

to undergo routine veterinary procedures (see **section 13.4**). **Figure 4.3** shows, in diagrammatic form, how this sort of learning takes place.

Operant conditioning refers to the technique of using reward and punishment to modify an animal's behaviour (Pearce 2008). Therefore it differs from classical conditioning in that the animals are learning about their responses (or, more exactly, about the consequences of their responses) rather than about stimuli. It is achieved by pairing the animal's response with a **reinforcer**, which is simply any event that increases the probability of the response, or **punishment**, which decreases the probability of the response. The reinforcer is referred to as a **positive reinforcer** if it follows the response (for example, the provision of a food reward) and a **negative reinforcer** if it involves the removal of a stimulus (for example, turning off an electric shock). Experimental and anecdotal evidence suggests that animals anticipate the reinforcer, and will learn different responses for different reinforcers, suggesting that the reinforcer acts as a US (see **Chapter 7**).

As with classical conditioning, it is likely that operant conditioning of zoo animals occurs informally or semi-formally all the time (for example, keepers 'rewarding' animals for doing the required

---

[5] 'Neutral' here is simply meant to imply that the stimulus is not one that the animal would normally encounter and therefore presumably has no particular significance for the animal. Examples might include the noise of a buzzer or clicker, or a light coming on.

Figure 4.4 Animals performing shows for the public, such as this killer whale *Orcinus orca* at Kamogawa Sea World, are trained through classical and operant conditioning techniques (Photograph: Jeroen Stevens)

Figure 4.5 Training a new behaviour involves building an association between a command—the conditioned stimulus (S2)—and an already occurring behaviour—the unconditioned response (R1). When the keeper gives the command, he or she expects the animal to perform the appropriate behaviour—the conditioned response (R2). If the animal reacts appropriately after the command, it is reinforced with the reward (food). This increases the likelihood that it will perform the behaviour again after the command. Alternatively, if the animal does not perform the appropriate behaviour, it will not receive the reinforcer (so is either ignored or punished), which will reduce the likelihood that it will perform the 'wrong' behaviour after the command in the future. Sometimes, prior to training, a secondary reinforcer (also referred to as a 'bridge') is associated with the primary (naturally occurring) reinforcing stimulus; for example, a whistle is blown when the animal is eating, so that an association is made between the whistle and food. In this case, if the animal reacts appropriately after the command, it is reinforced with the secondary reinforcer (whistle) and then the reward (food). It should be noted that punishments are not necessarily 'harmful' and that an absence of a reinforcer (i.e. time out) can itself be punishing.

thing, or perhaps animals learning that certain behaviours draw crowds, and so on). In a formal way, both operant and classical conditioning techniques have long been used in zoos, aquariums, and circuses to train animals to perform shows for the public (**Fig. 4.4**). Nowadays the main use of these techniques is in **positive reinforcement training (PRT)**, during which animals are trained to undergo veterinary inspection, to move from enclosure to enclosure, and to undertake other husbandry activities. The way that this is achieved is shown diagrammatically in **Fig. 4.5** and there is more about this technique in **section 13.4**.

Before leaving associative learning, we should mention imprinting, which is probably no different in mechanism from the sorts of conditioning we have just considered, but which is usually used to describe the special case of the formation of an attachment between a young animal and its parents (filial imprinting). This is the stage at which the young animal can learn the species to which it belongs and who its relatives are, and this can have consequences

for its later choice of a sexual partner (sexual imprinting). In many animals, particularly birds, there is a particularly sensitive period soon after hatching or birth when imprinting is most likely to occur. For this reason, hand-rearing, or rearing in the absence of **conspecifics**, runs the risk of producing animals who fail to imprint appropriately or, worse still, imprint on their keeper.[6] Small felids reared without conspecifics, for example, show extreme aggression to potential mates and are unlikely to reproduce (Mellen 1992; see also **Box 9.6**).

In birds, especially where artificial rearing is necessary, the use of models may help appropriate

---

[6] A famous example of imprinting on keepers was Chi-Chi, the iconic female giant panda *Ailuropoda melanoleuca* who lived in London Zoo in the 1960s and would not mate with An-An, the male who was brought at great cost from Moscow Zoo in the hope of siring a cub.

imprinting. For example, young sandhill cranes *Grus canadensis* imprinted on crane-like puppets, or even humans dressed up in crane costumes, learned to associate appropriately with wild cranes when later released into the wild (Horwich 1989).

Other kinds of learning

As we mentioned in the previous section, many animals are perfectly capable of learning much more complex things than only associations between events and, while this ability is not much used or studied in the zoo setting, anyone working with animals should be aware of their potential abilities.

'Discrimination learning' refers to the ability of animals to distinguish between different kinds of events or objects. In some cases, they are able to assign objects to categories. Many of these studies have involved animals such as pigeons, chickens, and monkeys in laboratory settings, but studies in zoos (**Fig. 4.6**) have included elephants and sea lions—with the sealions needing fewer trials than the elephants to learn the discriminations (Savage *et al.* 1994). To some extent, we can regard these animals as forming concepts. Pigeons seem to be quite good at this (Herrnstein 1979), but gorillas less so (Vonk and MacDonald 2002), which warns us that the distribution of **cognitive** abilities (i.e. those which involve mental processes) through the animal kingdom is much more complicated than we might expect.

Other aspects of complex learning include the ability of animals to understand time, number, and the order in which objects are placed, their ability to learn to recognize their image in a mirror, and their ability to form a cognitive map of an area. The evidence for all of these has come predominantly from animals in laboratories, but there is no reason, in principle, why some should not also be studied in the zoo, which would substantially increase the comparative value of learning studies. For example, Lonsdorf *et al.* (2009) used groups of chimpanzees *Pan troglodytes* and gorillas *Gorilla gorilla* at Lincoln Park Zoo, Chicago, to compare

Figure 4.6 Apparatus to test discrimination learning, being used here with Goeldi's monkey *Callimico goeldii*. The animals are rewarded if they successfully go to the black, rather than the white, squares. (Photograph: Paignton Zoo Environmental Park)

the two species on their acquisition of the same tool-using task, and Taubert (2010) investigated how black-handed spider monkeys *Ateles geoffroyi* at Symbio Wildlife Park, Australia, processed facial images of people and other spider monkeys.

Much of the experimental work in animal learning has attempted to describe how an individual learns as a result of its own experience, but recent research has also highlighted the importance to many animals of social learning, through which they can effectively acquire learning from other individuals through processes such as **imitation**[7] and **stimulus enhancement**. Famous examples of these include blue tits *Cyanistes caeruleus* pecking open the foil caps of milk bottles (Fisher and Hinde 1949) and Japanese macaques *Macaca fuscata* washing potatoes in the sea (Kawai 1965), both of which appear to be the result of animals watching what others are doing.

Social learning can lead to the establishment of culture,[8] one of the most famous examples of which is the different local behavioural traditions (for example, termite fishing, cracking nuts with stones, etc.) of different chimpanzee populations (Whiten *et al.* 1999) (**Fig. 4.7**). Again, research on social learning can profitably be undertaken in zoos. The 'artificiality' of zoos presents animals with opportunities for devising novel behaviours, such as using a

---

[7] **Imitation** refers to an animal copying another's motor pattern. **Stimulus enhancement** occurs when an animal's attention is drawn to a particular stimulus.

[8] Culture, in this context, refers to the non-genetic transmission of behavioural change across generations.

Bossou
Guinea

Kibale
Uganda

Budongo
Uganda

Tai Froest
Ivory Coast

Gombe
Tanzania

Mahale
Tanzania
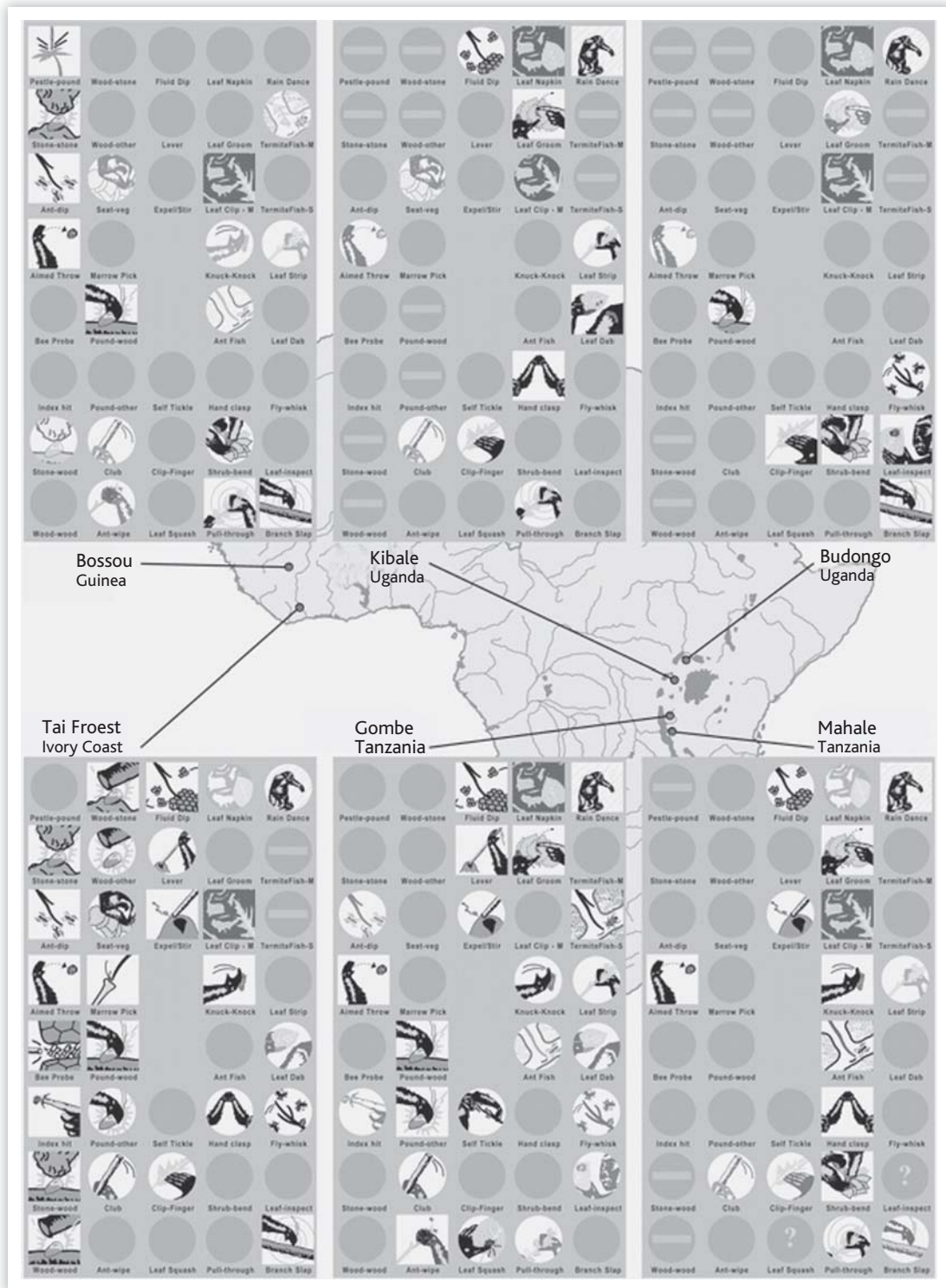
Figure 4.7 Cultural differences in tool use across different populations of chimpanzee *Pan troglodytes* (From Whiten *et al.* 1999)

Figure 4.8 A ringtailed lemur *Lemur catta* dipping its tail in the moat that surrounds Lemur Island at Chester Zoo. The lemurs then drink the water from their tails. This behaviour apparently spread in the group through social learning. (Photograph: Geoff Hosey)

wooden splinter for cleaning nails, as in a mandrill *Mandrillus sphinx* at Chester Zoo (Pansini and de Ruiter 2011). These behaviours may then spread through the group. An example is tail immersion in ringtailed lemurs *Lemur catta*, which is performed by some individuals in an island-living colony at Chester Zoo, UK (Hosey *et al.* 1997) (**Fig. 4.8**). Indeed, cultural traditions can be induced experimentally, as in, for example, colobus monkeys *Colobus guereza* at Paignton Zoo Environmental Park, UK, which acquired habits of pushing an apparatus for food in one group and pulling it in the other (Price and Caldwell 2007), or ruffed lemurs *Varecia variegata* at Zoo Atlanta lifting or swinging a hinged door to obtain food (Stoinski *et al.* 2011).

4.1.3 Motivation

We know both experimentally and anecdotally (and, indeed, personally) that individuals vary from occasion to occasion in the likelihood that they will undertake particular behaviours, including learning tasks. This variability, which also occurs between individuals, is often referred to as 'motivation' and is generally thought of as some kind of internal process that influences the likelihood of whether or not the animal will do the behaviour. In the past, motivation has often been seen in terms of some kind of drive or energizer that activates specific behaviours, but while this notion has some intuitive appeal, it fails to account for what is known about variability in responsiveness and has largely been abandoned. We now see motivation more as a decision-making process in which the animal prioritizes the behaviours it must do and switches between them according to these priorities. Factors such as hormones, the attractiveness of a stimulus, and the length of time since the animal last did a particular behaviour can all affect the way in which the behaviour is prioritized.

What happens if the animal is unable to perform the behaviour that it is highly motivated to do? This leads to frustration and, if this is maintained over a long period, it can have adverse effects on the animal's welfare (see **Chapter 7**). Similarly, if the animal is highly motivated to perform two mutually conflicting behaviours—that is, if it cannot do them both, such as, for example, approaching, but also avoiding, a novel object that increases both curiosity and fear—then motivational conflict can result and this too can have welfare implications if it carries on over a long period. In the short term, unusual behaviour such as **vacuum activities** and **displacement behaviour** give us clues about the motivational state of the animal. But frustration and conflict over the long term can lead to the development of **abnormal behaviour** (see **section 4.4**), which tells us that the animal has had poor welfare in the past and alerts us to the possibility that it is still suffering poor welfare. This is an important area of captive animal management and is considered in more detail in **section 4.4**.

How an animal responds to stimuli and events is, then, a consequence of both its genetic makeup and its past experience and learning about these things. Because different individual animals differ from each other in both of these components, it should not surprise us too much that they also may differ from each other in the ways in which they respond. Sometimes, this can lead to consistent individual differences between animals in the ways in which they behave and which cannot be attributed to just their age or their sex. This topic is explored more fully in **Box 4.2**.

Box 4.2   INDIVIDUAL DIFFERENCES IN BEHAVIOUR: THE INFLUENCE OF PERSONALITY

Most zookeepers, at some stage, will talk about the animals in their care using the same sorts of term that people use to describe one another, such as 'aggressive', or 'cautious', or 'shy'. In other words, they are ascribing personality traits to individual animals. But to what extent is it valid to use the term '**personality**' (or, better still, 'animality')[9] to describe consistent behavioural responses in animals, and how useful is a knowledge of animal personality in the zoo environment?

We have seen already in this chapter how individual differences in behaviour between animals of the same species can arise as a result of experience, or can be attributed to the animal's age or sex. There is now, in the scientific literature, widespread use of the word personality to describe stable and consistent behavioural styles or temperament traits in a range of different **taxa** (see Briffa and Weiss (2010) for a very readable overview, Freeman and Gosling (2010) for a summary of studies on non-human primates, and Gosling (2001) for a comprehensive review). There are now a number of studies providing compelling evidence for a strong genetic basis for personality traits in animals, in animals ranging from great tits *Parus major* (for example, in work by Van Oers *et al.* (2004) and Dingemanse *et al.* (2002)) to vervet monkeys *Chlorocebus pygerythrus* (Fairbanks *et al.* 2004). Personality traits have also been described in many other taxa, including numerous species of fish (Sih *et al.* 2004; Réale *et al.* 2007) and some invertebrates, such as octopus (Sinn *et al.* 2001) and hermit crabs (Briffa and Twyman 2011; Mowles *et al.* 2012). An understanding of personality can have implications for the captive management of wild animals, since it can help to explain why different individuals respond to captivity in different ways and therefore may have different welfare concerns (see **section 7.1.1**), but there may also

be consequences for conservation. In the longer term, zoo environments may select those individuals whose personality is best fitted to captivity. In cheetah *Acinonyx jubatus*, Wielebnowski (1999) used observer and keeper ratings to assess individual behavioural variation in forty-four adult captive-born animals. She found that just three temperament components—'tense–fearful', 'excitable–vocal', and 'aggressive'—accounted for 69 per cent of observed variation in behaviour (**Fig. 4.9**). Traits such as aggression or a high level of activity, for example, may be more likely to be selected against in zoos, because such animals will be more difficult to manage and may do less well in captivity (McDougall *et al.* 2006). Indeed, Hansen and Møller (2001), have suggested that animal welfare could be improved not by modifying the environment to fit the needs of

Figure 4.9 Personality components such as 'tense–fearful' are derived from keeper ratings and we would expect them to correlate with behavioural measures such as the time taken (latency) to approach a novel object, as seen here when a cheetah was given a traffic cone. (Photograph: Paignton Zoo Environmental Park)

---

[9] Animality featured in the title of a symposium at the University of Stirling in 2005: *Animality! Personality in Animals: An International Symposium on the Importance of Personality and Temperament in Understanding Behaviour*.

captive animals, but by modifying or selecting the animals kept in captivity so that they are better adapted to farm, or laboratory, or zoo conditions. In their work on captive mink *Mustela vison* in fur farms, for example, they found that fur-chewing behaviour can be reduced simply by selection, apparently with no negative effects (Malmkvist and Hansen 2001).

Differences in reproductive performance between individuals may also sometimes be related to personality differences. Tetley and O'Hara (2012) suggest that personality assessment can be used in zoos to help identify possible reasons for the reproductive failure of individual animals, and highlight the need for further research into areas such as pair compatibility. Carlstead *et al.* (1999a) looked at personality traits[10] in captive black rhinoceros *Diceros bicornis* and found that behavioural scores grouped into the overall trait 'dominant' were negatively correlated with reproductive success for males. Moreover, the higher the female's score in the 'dominant' category relative to her male partner, the greater the breeding success of the pair. Powell *et al.* (2008) have identified a relationship between 'shyness' and socio-sexual behaviour in female giant pandas *Ailuropoda melanoleuca*, with timid females showing poorer socio-sexual peformance. In contrast,

bold or dominant female giant pandas were less likely to behave agressively towards males during the breeding season.

But modification of personality traits in captivity, whether intentional or unintentional, may have consequences for animals intended for eventual **reintroduction** back into the wild. Only a small number of studies have attempted to consider the relationship between personality and survival after reintroduction (for a review, see Watters and Meehan 2007). For example, Bremner-Harrison *et al.* (2004) looked at personality assessment as a predictor of survival in the wild of captive-bred swift foxes *Vulpes velox*. This study concentrated on an assessment of boldness versus timidity; the results clearly showed that bold foxes were less likely to survive during the immediate post-release period. But while boldness is detrimental to short-term survival in swift foxes, in bighorn ewes *Ovis canadensis* Réale and Festa-Bianchet (2003) found that selection favoured the bold: ewes categorized as non-docile or bold were less likely to be preyed upon by cougars.

For readers interested in using behavioural profiling in studies of zoo animals, the BIAZA Research Group provides guidelines (Pankhurst *et al.* 2009, available from the BIAZA website **http://www.biaza.org.uk**).

4.1.4 Functional explanations of behaviour

Functional explanations attempt to understand how behaviours evolve to increase the fitness of the animal—in other words, they increase the animal's survival prospects and reproductive success. The most successful approach to this has been **behavioural ecology**,[11] which examines the evolution of behaviour within the context of the animal's ecology. Behavioural ecology is based on

a number of key concepts, the most important of which are:

- the gene-centred approach, within which the effects of natural selection on the gene are given prominence, rather than its effects on whole bodies;

- optimality, which recognizes that there are costs, as well as benefits, in performing particular behaviours and thus that evolving efficient

---

[10] Carlstead's work was carried out as part of a wider initiative, known as the Methods of Behavioural Assessment (MBA) project. This cross-institutional research initiative by twelve leading North American zoos is discussed in more detail in **Chapter 14** on research in zoos.

[11] Early in its career, behavioural ecology was often referred to as 'sociobiology'. It came to prominence particularly through Edward Wilson's classic text, *Sociobiology: The New Synthesis* (1975), which is still worth a read now, 40 years later.

ways of behaving involves some sort of trade-off between these;

- the recognition that there are a number of different ways in which behaviours can be done, so that alternative strategies are available to achieve the end of raising fitness.

This is an area of behavioural biology that has grown enormously in the last three decades and, again, we do not have space to do more than give a very brief overview of this subject here. Most importantly, however, we can point out that behavioural ecology has been hugely successful in providing explanations of the evolution of many behaviours that were previously quite puzzling, and that it has led us to view what animals do in a very different way than was done before. The following are some examples.

Altruism and cooperation

Helping somebody else, which potentially lowers one's own fitness while increasing that of the other, is challenging to explain. But although these behaviours (such as alarm calls, division of labour, cooperative hunting, feeding sick and injured members of the group, and many others—**Fig. 4.10**) look **altruistic** at the level of the animal that is behaving, at the level of the gene, they can actually be seen to be selfish and therefore we can better understand how they evolve.

At least two explanations are available:

- kin selection—that is, by behaving altruistically to relatives, the animal is furthering the fitness of individuals who have copies of the same genes as itself, through relatedness (originally proposed by Hamilton (1964));
- reciprocity—that is, behaving altruistically to those individuals who will, at some stage, pay back the good deed (originally proposed by Trivers (1971)).

Because of these explanations, we can start to understand why, for example, helping is often seen in groups of relatives and why an animal may

Figure 4.10 Meerkats *Suricata suricatta* are social mongooses that live in troops made up of family groups, where there is high genetic relatedness. They show a variety of altruistic and cooperative behaviours, including acting as sentinels to watch out for, and warn the rest of the group about, approaching dangers. (Photograph: Sheila Pankhurst)

behave more cooperatively with some individuals than with others.

Finding food

Finding and processing food is not a simple matter of going looking until something edible is found and then eating it. Animals are confronted with decisions that they must make during their foraging, and they are also subject to a number of constraints which limit the sorts of decision that they can make.

So, what sorts of decision must foraging animals make? If we apply the 'optimality' concept, we realize that the outcome is not the maximum that an animal can do or achieve, but rather the

optimum. In the case of food-finding, this might mean something like the best food return that can be obtained for a given amount of energy expended in finding or processing it. This means that the decisions with which animals are faced are essentially economic, and are to do with optimizing a particular currency[12] in the face of particular constraints. Examples of currencies are things such as the rate of food intake, the efficiency with which the animal collects food, and delay of starvation. Examples of constraints might be the need for minimum daily levels of particular nutrients, or the physical size of the animal's stomach.

Now consider an animal that has two kinds of prey: one is small, but can be processed quickly (that is, it has a small 'handling time'); the other is large, but takes a lot of time and energy to process. Which prey should this animal choose? The answer is that it should choose the most 'profitable' prey—that is, the prey with the greatest energy gain per unit handling time. What if the big prey are more profitable, but the animal encounters small prey first? Should it eat the small prey, or should it ignore it and look for bigger prey? Now, the answer is that it should only eat the small prey if what it gains from doing this is greater than what it would gain from rejecting it and looking for larger prey. Quantitative models can be constructed to show the circumstances (in terms of search time, handling time, and energy gain) in which this animal should make that decision. These decisions, and others like them ('Should I stay where the food is, or move out with each piece even though that takes energy, but reduces my risk of being caught by a predator?'), are unlikely to be cognitive decisions that the animal thinks about and works out, but probably involve the application of 'rules of thumb'. But our quantitative models are essentially hypotheses that give us predictions about these rules of thumb, and therefore are a powerful way of understanding

how behaviour and ecology have been shaped by evolution.

Mate selection

One of the most direct effects of behaviour on fitness comes when animals are faced with making reproductive decisions. Mating behaviour should not only provide a mate, but it should also provide the best possible mate. But what does that mean? Does it mean the best fighter (to defend the young), or the best provider of food (so, someone with a good territory perhaps), or does it mean the most healthy individual (**Plate 4.1**)?

Trivers (1972) was one of the first to realize that male animals were likely to have different evolutionary priorities to female animals, and that this was likely to lead to conflicts of interest between the sexes. In its most basic form, this conflict starts because males produce plenty of sperm (which are energetically cheap to produce) and therefore they can best increase their lifetime fitness by mating with as many females as possible, but deserting them and therefore imposing the costs of raising young on the females. Females, who produce small numbers of ova (which are more costly to produce), can best increase their fitness by caring for a smaller number of young and making sure they survive. Thus, the evolution of mating systems can, to some extent, be seen as a kind of 'arms race' between males and females, each trying to minimize their costs and maximize their benefits at the other's expense; this can lead to males and sometimes siblings providing care for offspring.

Out of all of this come what look to us like different sorts of mating systems.

- **Monogamy**—a pairing between one male and one female, particularly in those species among which male desertion is not profitable because females are unable to raise the young alone (for example, many birds).

---

[12] In terms of an animal's economic decisions, currency refers to the costs and benefits operating on the animal, while constraints are the behavioural and physiological mechanisms that limit what the animal can do.

Figure 4.11 Polygny, where one male mates with multiple females, can lead to the evolution of larger body size in males, as seen here in these hamadryas baboons *Papio hamadryas*. (Photograph: Geoff Hosey)

- **Polygamy**—where a member of one sex has multiple mates. This then includes:
  - **polygyny**—within which one male may mate with many females (**Fig. 4.11**), particularly in species among which females are able to raise young with little male input (for example, many mammals, in which gestation and lactation facilitate male desertion);
  - **polyandry**—in which one female may mate with a number of males (this is rare, but occurs in some species such as the northern jacana *Jacana spinosa*, a species of tropical wading bird).
- **Promiscuity**—within which both males and females have multiple sexual partners. Modern molecular techniques have allowed us to see that more species than we expected are promiscuous, even if at surface level they look monogamous or polygamous, because the DNA shows us who an individual's real mother and father are—and often they are not the ones who are bringing the young animal up (see **Table 9.1**).

Behavioural ecology proposes fascinating explanations for other aspects of animals' lives, such as the evolution of signals and strategies for aggression and submission. We recommend that, if you are interested in this area, you should read a good textbook such as Krebs *et al.* (2012) or Alcock (2009).

4.2 Animal behaviour in the zoo

The body of theory that we briefly reviewed in **section 4.1** helps us to interpret what we see animals doing in the zoo and why they are doing it. An understanding of behaviour underpins much of the management of zoo animals, from interpreting their welfare (**Chapter 7**) to organizing the structure of breeding groups (**Chapter 9**).

But understanding theory is not enough on its own. We also need basic descriptive information about the behaviours that the animals do. Very often, this information is not available from the wild, and zoo studies represent most of what we know about many species. We can acquire this kind of information by looking at how zoo animals respond to physical and social stimuli in their environment, and also simply by observing and cataloguing what they do.

4.2.1 Stimuli and responses

The physical environment

The environments in which animals live may vary temporally (for example, with day–night cycles, lunar cycles, seasons) and spatially (for example, according to different habitats and microhabitats within the animal's home range). Stimuli associated with these aspects of the environment are used by the animal in choosing appropriate responses. The zoo environment may, or may not, fall within the range of spatial and temporal variability that an animal experiences in the wild, but we would clearly expect that the more overlap that the zoo environment has with the animal's natural environment, the better able the animal will be to show appropriate responses to that environment. It follows, then, that we can provide better environments for captive animals if we know which stimuli are most important for them.

Surprisingly little research has been done on the stimulus sensitivities of zoo animals compared with laboratory and farm animals. It has been shown, for example, that routine procedures

and items of laboratory equipment produce **ultrasound** that humans cannot hear, but which many other animals can (Sales *et al.* 1999), but virtually nothing is known about sources of ultrasound in the zoo. Clearly, this could have welfare implications, because ultrasound can cause stress in laboratory rodents (Sales *et al.* 1999). We also know little about the ways in which many zoo animals use stimuli, often in more than one **modality**, to explore and use their environment. For instance, manta rays *Manta birostris* were observed at Oceanário de Lisboa in Portugal, and were found to use a combination of olfactory and visual stimuli as well as a cognitive map to locate food in their tank (Ari and Correia 2008).

A good example of the way in which stimulus information can be used to improve the management and welfare of zoo animals is the study by Dickinson and Fa (1997) of the spiny-tailed iguana *Oplurus cuvieri* in Jersey Zoo (**Fig. 4.12**). In these and many other reptiles, ultraviolet (UV) light from sunlight is used in the synthesis of vitamin D, which, in turn, is necessary for proper bone development and the production of viable eggs. However, provision of UV light sources in captivity does not always successfully address this problem. Dickinson and Fa (1997) showed that this was because the iguanas prefer to bask under the ordinary incandescent white lights, which are warmer than the UV lights; this then led to the recommendation that combined UV and hot light sources should be used to ensure that the animals get sufficient exposure to UV light (see **section 6.2.3**).

The social environment

Social stimuli (for example, stimuli from conspecifics) are also important in guiding behaviour because all animals in the wild live within a social context, even those traditionally labelled as 'solitary'. When social stimuli from one animal bring about changes in behaviour in another, we usually consider that communication has taken place and,

Figure 4.12 Spiny-tailed iguanas *Oplurus cuvieri* in captivity need exposure to UV light, but prefer to bask under ordinary incandescent white lights because they are warmer. (Photograph: Sheila Pankhurst)

in many cases, the stimuli have become highly ritualized (that is, have been made stereotyped[13] and 'bright' through evolutionary processes) into signals that are obvious even to us. Notice that causal explanations of why an animal gives a signal (for example, a male may give a mating signal because of the combined presence of high levels of hormones internally and a female externally) are at a different level from functional explanations (for example, the male evolves a signal that exploits aspects of the sensory modality, such as colour, that the female favours in an attempt to manipulate her into mating). Understanding the signals that different species produce starts at a descriptive level by including

---

[13] The term 'stereotyped' is used here to describe the process by which ritualized behaviours show an apparently fixed form and are sometimes repetitive. Unfortunately, the same word is used to describe some abnormal behaviours (see **section 4.4.3**) that also have fixed form and repetitiveness, but which otherwise have nothing in common with ritualized behaviours.

them in an ethogram (**section 4.1.1**). Deciphering what the signals mean is another matter entirely, but can yield important knowledge. Analysis of the vocalizations of giant pandas *Ailuropoda melanoleuca* at the Giant Panda Conservation Centre in China and San Diego Zoo revealed that male bleats give reliable information about their androgen levels, which is of potential use in their captive management (Charlton *et al*. 2011).

Opportunities for social interaction (that is, the exchange of communication) among animals are influenced by the structure and organization of the social group (for example, the number and type of different age/sex classes, and the dispersion of individuals through the habitat). These, in turn, are subject to evolutionary processes. Again, the range of social structures of any particular species maintained in zoos may overlap to different extents with those seen in the wild, and therefore social behaviour may be quantitatively, and possibly even qualitatively, different from that in the wild. Because of this, social behaviour is often used as an indicator of whether the zoo environment is affecting the welfare of the animal (see **Chapter 7**) and the manipulation of social behaviour can be used as an **environmental enrichment** to improve welfare (see **Chapter 8**).

4.2.2 Descriptive studies

Some studies of the behaviour of zoo animals are designed to collect basic data on what the animals do, how they distribute their behaviours through time, and how they interact with group members. We can generally call such studies descriptive studies, because they describe the behaviour of the animals in a quantitative way, but the best ones nevertheless follow proper scientific practice in terms of testing hypotheses or answering specific questions. Many of the species held in zoos have never been studied systematically in the wild, so zoos offer important opportunities to find out about the behaviours of the animals. (There is more about this in **Chapter 14** on 'Research'.)

Such studies may take this lack of information as their starting point, so their aim is to find out as

Figure 4.13 Some species, like this Matschie's tree kangaroo *Dendrolagus matschiei*, are difficult to observe in the wild and much of our knowledge of their behaviour comes from zoo studies. (Photograph: Geoff Hosey)

much as possible about the animals' behaviour. A good example of this sort of study is the description by Hutchins *et al*. (1991) of the behaviour of Matschie's tree kangaroo *Dendrolagus matschiei* (**Fig. 4.13**) at Woodland Park Zoo in Seattle, USA. Tree kangaroos are poorly known in the wild because of their rarity and **arboreality**, which makes observation difficult. Hutchins *et al*. (1991) started by compiling an ethogram of behaviours, using published work and their own observations. They spent 165 observation hours watching a group of four kangaroos and were able to quantify their social interactions (most frequent were approach and nose contact) and to detect quantitative differences in behaviour between males and females.

Other studies may concentrate on one or more specific behaviours that may be of interest as much because they inform behavioural theory as for their impact on animal management. There are plenty of examples of such studies, ranging from seasonal changes and circadian rhythms in koalas *Phascolarctos cinereus* (Benesch et al. 2010) and the breeding behaviour of platypus *Ornithorhynchus anatinus* (Hawkins and Battaglia 2009), both at Taronga Zoo in Sydney, to social network analysis of chimpanzees at Edinburgh Zoo (Clark 2011a) and social behaviour of ring-tailed coatis *Nasua nasua* at Chester Zoo (Romero and Aureli 2007).

4.3 Behavioural response to the zoo environment

Many behavioural studies in zoos are not designed particularly to obtain basic information about the species, but are more applied, in that they ask questions about how the animal's behaviour is altered by the zoo environment. Such studies are important for a number of reasons:

- they can alert us to welfare issues if the behaviour deviates substantially from what we would expect to see (see **section 4.4**);
- they can help us to ensure that behavioural diversity is not being lost through long-term adaptation to captivity;
- they can help us to find ways of providing exhibits that show wild-type behaviours and thus provide a better experience for the public;
- they can help us to evaluate the validity of those studies that do use zoo animals to test behavioural theory.

Many more of these sorts of applied behavioural studies have been undertaken in the last 20 years or so, but it is still the case that most are done on primates (Melfi 2005), and as we progress through the other mammals, birds, **herps**, fish, and invertebrates, the studies become fewer and fewer.

We have to start by asking what we mean by the 'zoo environment'. Clearly, there are a great many possible variables here that could influence behaviour. Therefore it is convenient to think of them under three subheadings: the physical environment, the social environment, and environmental change.

4.3.1 The physical environment

Enclosures

One potentially important variable in the physical environment is the absolute amount of space in which the animal has to live. Zoo enclosures are mostly smaller than the home ranges that animals occupy in the wild and, at least in Carnivores, home range size is a significant predictor of abnormal behaviours such as **stereotypy** (Clubb and Mason 2003) (see **Box 4.4**), which suggests that restricted space might be a causal factor in stereotypy development. So what effects on behaviour does restricted space have?

One way of answering that question is to compare animals in enclosures of different sizes. This is more difficult than you would expect, because different enclosure sizes usually have different furnishings, and accommodate social groupings of different size and composition. For this reason most comparisons have been of laboratory or farm populations, where variables other than enclosure size can be more easily controlled. Results generally suggest that small enclosures can adversely affect welfare—for example, collared peccaries *Pecari tajacu* were more aggressive in smaller enclosures (da Nogueira et al. 2010)—but note that differences in enclosure size often entail differences in other enclosure variables such as complexity (see **Box 6.1**). When comparisons have been done in zoos, however, they suggest that different kinds of animal are affected differently, as we might suspect. For example, wolves *Canis lupus* spend more time resting in large than in small enclosures, but their behavioural diversity appears to be related not to cage size, but to group composition (Frézard and Le Pape 2003). But in Przewalski's horse *Equus ferus przewalskii*, **activity budgets** differed significantly between groups in different sizes of enclosure, and aggression, grooming, and pacing were higher in the smaller enclosures (Hogan *et al.* 1988).

Regardless of the absolute amount of space available to them, many animals appear to use the different parts of that space unequally. Some parts of an enclosure may be heavily used, while other parts are hardly used at all. A good example of this is the post-occupancy evaluation study by Blasetti *et al.* (1988) of wild boars *Sus scrofa* at Rome Zoo, Italy. They found that nearly two-thirds of the activity of the animals occurred in just two of nine roughly equivalent (in size) sectors. In **Table 4.2**, D is an area with a lot of mud and shade, used by the pigs

Area within enclosure	Usage by adults (%)	Usage by piglets (%)
A	2.8	3.3
B	3.1	5.3
C	21.8	29.65
D	44.75	35.75
E	6.1	6.1
F	4.2	5.6
G	7.85	9.3
H	3.3	2.45
I	6.1	2.55
Total	100.0	100.0

Table 4.2 The percentage of utilization of different areas of their enclosure by wild boars at Rome Zoo*

*From Blasetti *et al.* (1988). Reprinted with permission of Wiley-Liss Inc., a subsidiary of John Wiley & Sons Inc.

Note how much the pigs used areas C (in which they were fed) and D (an area of mud and shade).

for sleeping and resting, while C is where they were fed. Sectors A and B, which show low usage, were next to a service road, while G, H, and I were next to a visitor road. Thus, the pattern of enclosure usage is partly the consequence of the animals' natural preferences and behaviour, and partly a response to non-natural aspects of the zoo environment.

Similar conclusions can be drawn for cats (pacing mostly at enclosure edges where the animal is at an artificial territory boundary, but where it can see keepers and visitors approaching (Lyons *et al.* 1997; Mallapur *et al.* 2002)), for great apes (chimpanzees and orang-utans used upper areas of the enclosure, whereas gorillas prefer the floor (Ross and Lukas 2006; Herbert and Bard 2000), and for Round Island geckos *Phelsuma guentheri* (avoiding vertical glass walls, but preferring hiding places and sunlight (Wheler and Fa 1995)).

We should not be too surprised that many animals use different parts of their enclosures unequally, or that they may have preferences or aversions to particular structural features. These may reflect the basic

biology of the species, or alternatively may highlight inadequacies of the enclosure design. When chimpanzees and gorillas at Lincoln Park Zoo, Chicago, were to be transferred to new enclosures, their space usage at the old enclosure was used to help design the new one. As a result, space usage of both species changed in the new enclosures, and the chimps in particular showed a pattern of usage in line with the availability of the structural features in the new enclosure, suggesting that it more closely matched their preferences (Ross *et al.* 2009).

The general consensus now (although based mostly on primate research) is that the absolute amount of space is of less importance than the quality of that space, in terms of structural complexity. A multivariate survey of gorillas and orang-utans across forty-one different European zoos, for example, found that the activity levels of the animals were related to the number of animals in the group and the presence of both stationary and movable objects, but were not related to enclosure size or surface area (Wilson 1982). Laboratory studies show similar effects with rodents and small primates, in relation to which complexity is more important than enclosure size. In many zoos now, the move towards more **naturalistic enclosures** provides an increase in both complexity and absolute size (see **Chapter 6**), and, where comparisons have been made, the naturalistic enclosures are accompanied by more naturalistic behaviours. An example is a study by Hoff *et al.* (1997) of gorillas at Zoo Atlanta, USA, which found that the behaviour of the animals in outdoor naturalistic enclosures differed from their behaviour in the indoor holding area. In particular, aggression was reduced outdoors (**Fig. 4.14**), as were a number of other individual and social behaviours.

Before finishing this section, it is worth saying something about crowding (i.e. increasing the stocking density; see **section 6.3.3**), which occurs when too many animals occupy too small a space. Ethological theories of the 1960s perceived a simple relationship between crowding and stress-induced aggression (see, for example, Desmond Morris (1969) who saw a parallel between human aggression and that of confined
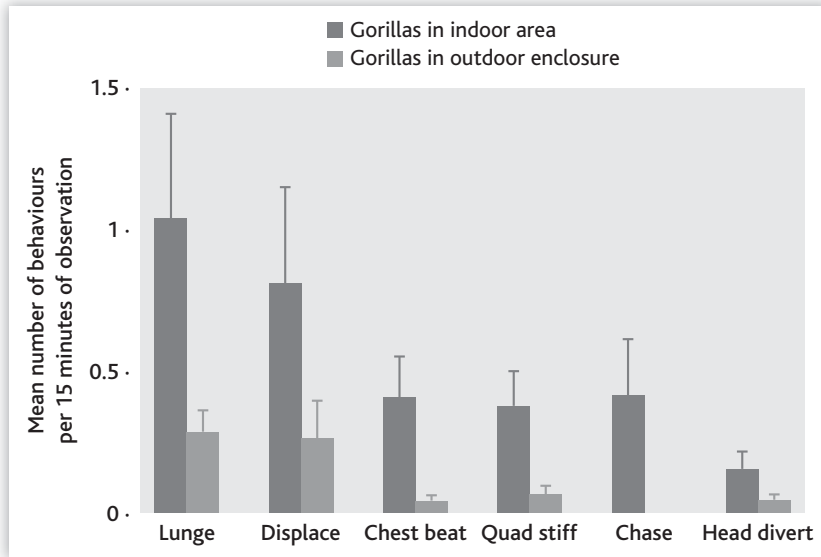
Figure 4.14 Comparison of the frequency of aggressive display behaviours in gorillas when they are in an indoor holding area compared with when they are in the outdoor enclosure. For each kind of display, the number of behaviours shown by the animals is significantly lower when they are outdoors. (Adapted from Hoff *et al.* 1997)

animals in the zoo). Several authors sought to confirm this relationship by studying aggression in zoo primates, an example being a study of rhesus monkeys *Macaca mulatta* in the Monkey Temple at Bristol Zoo, UK (Waterhouse and

Waterhouse 1971) (**Fig. 4.15**), which found high rates of aggression.

We now know that there is no simple relationship between crowding and aggression. Early experimental studies showed that social changes had
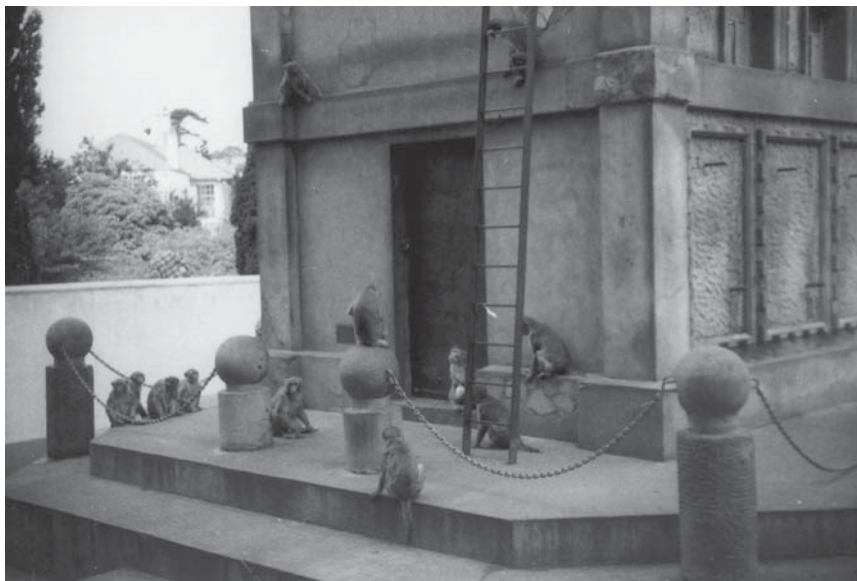
Figure 4.15 Rhesus monkeys *Macaca mulatta* in the Monkey Temple at Bristol Zoo, pictured here in 1964 (the structure is no longer used for housing animals). An early study of the effects of crowding on aggression was undertaken here. (Photograph: Geoff Hosey)

much greater impact on aggression than environmental changes (Southwick 1967), and more recent studies have demonstrated that chimpanzees *Pan troglodytes* (Nieuwenhuijson and de Waal 1982; de Waal 1989, Caws and Aureli 2003), bonobos *Pan paniscus* (Sannen *et al.* 2004), and rhesus monkeys (Judge and de Waal 1997) cope with temporary crowding (such as being brought into indoor winter quarters) through behavioural tension-reducing mechanisms, such as an increase in grooming and/or a decrease in aggression. More recently still, conflict avoidance has also been shown in tigers *Panthera tigris* temporarily housed in reduced space while their exhibit was undergoing renovation, with the result that reductions in both aggression and affiliation occurred, and persisted for a year even after return to their usual housing (A. Miller *et al.* 2011) (**Fig. 4.16**). In fish as well the relationship between stocking density and aggression is not simple: neon tetras *Paracheirodon innesi* and white cloud mountain minnows *Tanichthys albonubes* showed reduced aggression and increased shoaling in larger groups, and this was interpreted as improving their welfare (Saxby *et al.* 2010).

Food preparation and presentation

Food is a powerful motivator of behaviour in most animals, so we should not be surprised if the manner and timing of feeding affects behaviour in zoo animals. Timing of feeding can influence behaviour if its predictability allows the animals to anticipate it; this can lead to an increase in aggression—for example, in chimpanzees (Bloomsmith and Lambeth 1995) and Hamadryas baboons *Papio hamadryas* (Wasserman and Cruikshank 1983)—or stereotypic pacing—for example, in ocelots *Leopardus pardalis* (Weller and Bennett 2001). In laboratory stump-tailed macaques *Macaca arctoides*, experimental delay of routine feeding results in increasing levels of inactive alert agonistic behaviour, and self-directed and abnormal behaviours, during the anticipated pre-feeding time (**Fig. 4.17**) (Waitt and Buchanan-Smith 2001). Furthermore, the feeding routine may not be concordant with the natural activity cycles of the animal: for example, mid-morning feeding of brown lemurs
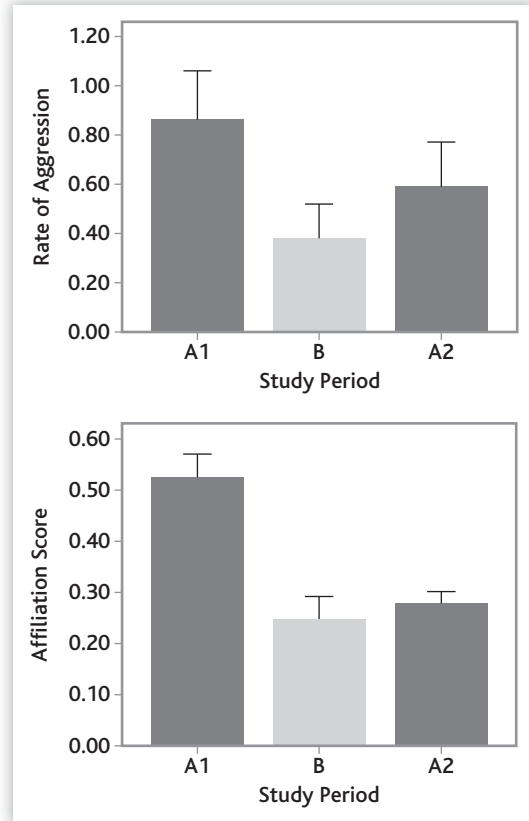
Figure 4.16 When tigers were temporarily housed in more restricted space (B) while their exhibit was being renovated, they coped with crowding by reducing interactions with other tigers, such as aggression and affiliation, and the lowered rates persisted for some time after return to their usual housing conditions (A2). (Adapted from A. Miller *et al.* 2011)

Eulemur fulvus disrupts their usual cathemeral pattern of activity[14] such that they feed at times when we would otherwise expect them to be inactive (Hosey 1989).

Behaviour is also strongly influenced by the way in which food is presented. For example, primates have traditionally been fed fruits and vegetables that have been chopped into small pieces, usually in the belief that this allows better and more equal distribution of food between individuals. But presenting whole foods to lion-tailed macaques *Macaca silenus* does not result in monopolization by individuals

---

[14] A cathemeral pattern of activity is characterized by sporadic periods of activity through the day and night.
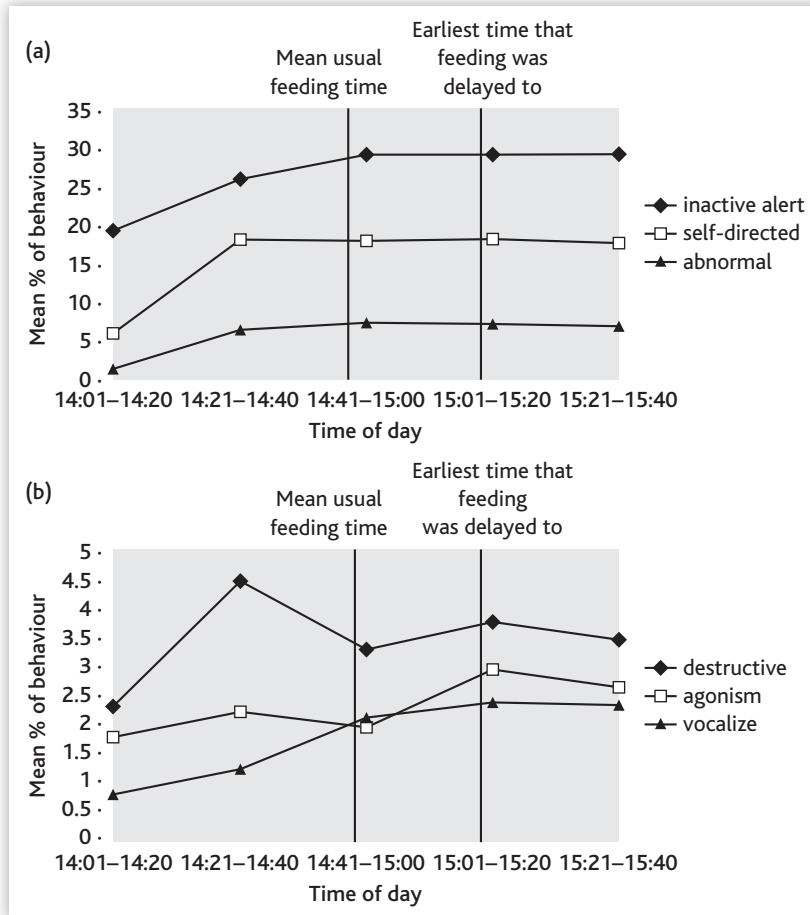
Figure 4.17 Anticipation of feeding in laboratory stump-tailed macaques *Macaca arctoides*. (a) Rates of inactive alert, self-directed, and abnormal behaviours rise in the period leading up to the time at which the animals are usually fed, and remain high if the animals are not fed on time. (b) Vocalizations also increase before the normal feeding time and remain high if feeding is delayed. However, destructive and agonistic behaviours rise before the usual feeding time, but then drop at about the time the animals are normally fed. If feeding is then delayed, these two behaviours start to rise again. (Adapted from Waitt and Buchanan-Smith 2001)

and individual feeding times increase (Smith *et al.* 1989). Similarly, multiple feedings of hidden food to leopard cats *Felis bengalensis* result in a decrease in pacing, but an increase in locomotory/exploratory behaviour (**Fig. 4.18**) (Shepherdson *et al*. 1993).

This is, of course, the basis of some kinds of feeding enrichment and this topic is discussed more fully in **Chapter 8**.

The zoo routine

Apart from feeding, few aspects of ordinary zoo routine have been investigated for their effects on behaviour. Zoo routines might include animal

capture (for example, cane toads *Rhinella marina* show elevated corticosterone when captured, which persists for some time after capture (Narayan *et al*. 2011)) and general noise (for example, increased noise levels resulted in greater agitation, such as scratching, vocalization, and manipulation of the exit door, in giant pandas at San Diego Zoo (Owen *et al*. 2004)). These examples give an indication of the variety of general zoo procedures which can affect behaviour (and there are others, such as enclosure cleaning, disturbance from park maintenance, capture or movement of neighbouring animals, and so on), but in general we have little quantitative data of what those effects are.

Figure 4.18 (a) Leopard cats *Felis bengalensis* are often inactive in captivity and may show stereotypic pacing. (b) In this experiment, the ration of food that the cats normally received only once per day was divided into four portions, so that the cats received four feeds irregularly every day. After a month, the four feeds per day were hidden within the enclosure. A significant decrease in pacing, and an increase in exploratory and locomotory activity (as indicated by the asterisks) was seen in the cats in both these conditions compared with when they received only one feed per day. ((a) Photograph: Jessie Cohen/Smithsonian's National Zoo; (b) Adapted from Shepherdson *et al.* 1993)
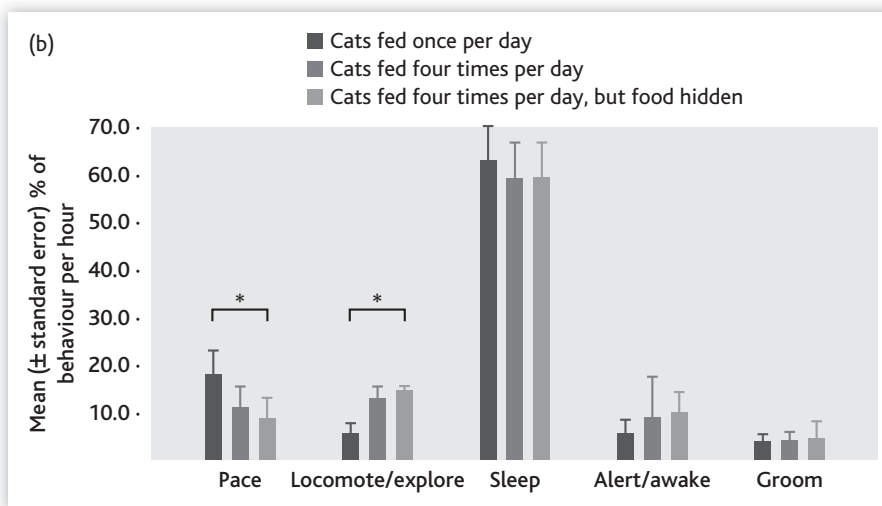
4.3.2 The social environment

The social environment consists of other living things, both human and non-human, whose presence and behaviour impacts on the behaviour of zoo animals. The effects of humans are dealt with in detail in **Chapter 13** and so will not be considered any further here.

Conspecifics

Much of behavioural biology is taken up with trying to understand how conspecifics interact with and influence each other. Here, we are concerned with situations in which the zoo environment may change the ways in which these interactions may naturally occur. An example of this is the way in which the animal is reared: hand-rearing is common in zoos for both mammals and birds, and there are numerous papers (for example, in the *International Zoo Yearbook*) on how this can be done. However, there are fewer studies on the behavioural effects of different rearing regimes. In its most extreme form, hand-rearing may be accompanied by social deprivation in infancy, and this may happen in non-zoo contexts before the animal reaches the zoo. Many zoo chimpanzees, for example, come from circuses, laboratories, and private ownership, and may have a variety of developmental histories. This can affect the social skills of these animals as adults, although some recovery of social skills is possible (Martin 2005).

Figure 4.19 Two silverback male Western lowland gorillas *Gorilla gorilla gorilla*, part of a successful bachelor group, engaged in social play. (Photograph: Kirsten Pullen)

Another way in which the zoo environment may influence intraspecific behaviour is through the maintenance of groups that differ in composition from that which usually occurs in the wild. This may result in a variety of effects which are not obviously predictable, as a few examples might show. Japanese macaques *Macaca fuscata* usually live in multi-male multi-female groups, within which females play an active role in the formation of mating pairs by soliciting some males and rejecting others. However, in a group of these animals at Calgary Zoo, within which there was a single male, one female instead prevented all the other females from mating, through harassment (Rendall and Taylor 1991). On the other hand, in spider monkeys *Ateles* spp. inter-male aggression can be a problem in zoo groups, primarily because these groups do not reflect the natural pattern in these species of male philopatry and female dispersal (Davis *et al.* 2009). Finally, female black-and-gold howler monkeys *Alouatta caraya* had more offspring, and more of those offspring survived, if the females were maintained in family groups rather than in a pair (Farmer *et al.* 2011), see also **Box 4.3**.

Studies such as these provide evidence that, for those species at least, the animals are best kept in naturalistic groupings. However, this can generate further consequences for some of the animals. An example of this is all-male gorilla groups, which are maintained at a number of zoos as a consequence of keeping breeding groups in as naturalistic a form as possible (i.e. polygamous harem groups). These 'bachelor' groups can show high group cohesion (**Fig. 4.19**), particularly in sub-adult animals (Stoinski *et al.* 2001). Both silverbacks and blackbacks in these groups may show different intensities of aggression in comparison with males in breeding groups (Pullen 2005). Of course, all the examples we have given so far are of primates, and we should not expect that other taxa will show the same effects. In a study of giraffes *Giraffa camelopardalis* at two different zoos, for example, Bashaw (2011) found that activity budgets and social interactions in female giraffes held in a single-sex group were similar to those housed in mixed-sex groups.

Group composition is related to group size—that is, to the number of animals in the group. In the wild, group size is the consequence of a number of different ecological and behavioural processes, some of which (such as the need to avoid predators and find food) are of less significance in the zoo environment. Consequently, we would expect greater flexibility to be possible in the sizes of captive groups, and this does seem to be the case for many species (Price and Stoinski 2007). Nevertheless, maintaining too many, or too few, animals in a group can have a negative impact on their health and behaviour. For example, small felids are often solitary in the wild, and housing them with conspecifics can increase stress and reduce reproductive success for the cats; conversely, reproductive success in **callitrichids** is impaired

Box 4.3 EFFECTS OF CONSPECIFICS: FLAMINGO BREEDING DISPLAYS

Flamingos are very social birds that can form flocks of up to a million birds during the breeding season. In zoos, their group sizes are a great deal smaller than this, and this has consequences for their breeding which is poor in small groups (**Fig. 4.20**) (Stevens 1991; Pickering *et al.* 1992). So what is it about group size that promotes breeding success in captive birds?
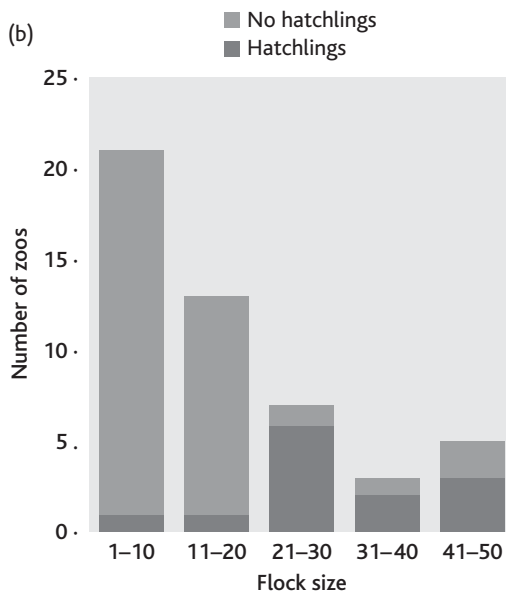
Figure 4.20 (a) Greater flamingo *Phoenicopterus roseus* group with mirrors to enhance apparent group size and stimulate breeding. (b) Success at breeding Caribbean flamingos *P.ruber* in zoos depends upon group size. These data, for the period 1983–1988, show that most zoos that keep the birds in flocks of more than twenty-one individuals produce hatchlings, whereas few of those that keep groups of fewer than twenty birds are successful. ((a) Photograph: Jeroen Stevens; (b) From Stevens 1991)

A study of Caribbean flamingos *Phoenicopterus ruber ruber* at the National Zoo in Washington DC (Stevens 1991) showed that group displays increased by 48 per cent when the flamingo flock size was increased from eighteen to twenty-one, and the synchrony of the displays increased by 100 per cent. Mounts, copulations, and the production of fertile eggs (the first ones in the group's history) also increased. Further addition of birds in subsequent years increased display activity even more (Stevens and Pickett 1994). Thus, although there may be other important factors in flamingo breeding, one of the most important is having enough birds in the flock to produce sufficient social stimulation through group displays. Similar effects are seen in other flamingo species, such as Chilean flamingos *P.chilensis* (Farrell *et al*. 2000).

This example emphasizes the importance of providing a suitable conspecific social environment for zoo animals.

when group sizes are too small, since fewer helpers are available to raise infants (Price and Stoinski 2007). Group size is also related to stocking density, so large group sizes may result in crowding, as we have already seen (**sections 4.3.1** and **6.3.3**).

Finally, animals may, for various reasons, be kept singly in zoos rather than in social groups. Few studies have investigated the behavioural consequences of this, although pairing primates as a form of social enrichment is well known in the laboratory world. A comparison of the behaviours of pair-housed with singly-housed tigers *Panthera tigris* showed that the paired animals displayed a wider variety of more naturalistic behaviours (De Rouck *et al*. 2005), suggesting that being singly housed adversely affected the behaviour of the animals. Singly-housed tigers rolled and played with objects by themselves more than the paired tigers did. This ambiguous result is difficult to interpret in terms of whether tigers should be housed singly or in pairs (see **Table 4.3**). In snow leopards *Panthera uncia*, there were no significant differences in the activity budgets and pacing behaviours of solitary-housed compared with socially-housed animals, although the latter showed social behaviours which (obviously) the singly-housed animals were unable to show (Macri and Patterson-Kane 2011).

Other species

Animals in zoos may encounter other species within their enclosures, contributing to **mixed-species exhibits** (**Fig. 4.21**), or they may see, or in some other way detect stimuli from, other species in other enclosures (see **section 6.3.3**). Mixed-species exhibits have a long history in zoos, and in general the mixture of species used is a relatively appropriate one of species that inhabit the same area in the wild and which (hopefully) do not eat each other. A number of descriptive accounts are available in the literature (Pochon 1998; Young 1998; Ziegler 2002; Dorman and Bourne 2010) but fewer quantitative studies have been carried out to see how mixed species interact with one another (**Plate 4.2**). Popp (1984) investigated aggression between ungulates of different species in mixed groups and found that the greatest amount of

Group	Pacing	Rolling	Flehmen	Playing
Pair without neighbours	4.67	0.15	0.19	0.36
Pair with neighbours	21.30	0.16	0.16	0.06
Single with neighbours	23.91	0.31	0.56	0.62

Table 4.3 Average percentages of time tigers spent in those behaviours that differed significantly between housing conditions*
*Data from De Rouck *et al*. (2005).

Note: Tigers without neighbours paced less than those with neighbours; single animals rolled on the ground, performed flehmen (an olfactory behaviour), and played more than paired tigers did.

Figure 4.21 A mixed group of wildebeest and springbok at Olmense Zoo. (Photograph: Jeroen Stevens)

aggression was between more distantly related species. Events such as births, mating behaviour, and animal introductions were the main triggers of aggression, and male aggression was one of the main features related to the success of the exhibit. Other studies (with primates) have found inter-specific affiliative interactions as well as aggressive and neutral interactions (Leonardi *et al.* (2010) on capuchins *Cebus apella* with squirrel monkeys *Saimiri sciureus*; Pearson *et al.* (2010) on orang-utans and siamangs *Symphalangus syndactylus*), and again we would expect different combinations of different species to get along with each other (or not) in different ways. Aquariums routinely display mixed-species assemblages, and little research has been undertaken on the consequences of this. Saxby *et al* (2010) investigated mixed-species groupings of some small fish species kept commonly in home aquariums, and found that angelfish *Pterophylum scalare* appeared to have a beneficial effect by reducing aggression of the smaller neon tetras and white-cloud mountain minnows, but we know very little about interactions in the large tanks which are a part of many modern public aquariums.

Sometimes, the different species are located in different enclosures, but may still be able to detect each other. Predators and their prey would not normally be housed in the same enclosure, but if they can see each other, we would expect this to be reflected in their behaviour. Stanley and Aspey (1984) studied the behaviour of five ungulate species at Columbus Zoo, housed in an African

exhibit where lions *Panthera leo* in a neighbouring enclosure (separated by a dry moat) were only visible if they came to the front of the enclosure. When the lions were visible, the ungulates spent less time with their heads down (for example, feeding, drinking, sniffing the ground) so as to spend more time being vigilant (**Fig. 4.22**).

It is unclear whether situations such as these have welfare consequences for the prey species (in this study, the authors thought not), but laboratory studies with small primates (cotton-top tamarins *Saguinus oedipus*) have shown that even the smell of predator faeces can result in what appears to be anxiety in the animals (Buchanan-Smith *et al.* 1993) (**Fig. 4.23**). On the other hand, tamarins show responses to a model bird being flown over their enclosure that are similar to those shown for environmental enrichment (Moodie and Chamove 1990), so this issue is by no means clear (see **section 7.3.1**).

4.3.3 Environmental change

The management and care regimens at zoos can often require changes to be made that might impact on the animals' behaviour. These changes may affect the physical or social environment of the animals, which, as we have just seen, may already have brought about some behavioural change in themselves. Once again, the literature is dominated by primate studies.

Changes in housing

The laboratory literature shows clearly that cage relocation can be stressful for primates (e.g. Mitchell and Gomber 1976; Line *et al.* 1989a; Schaffner and Smith 2005), but it is unclear how pertinent this is to zoo primates (because the zoo and laboratory environments differ in so many other ways) or indeed to other animal species. Moving leopard cats from barren home enclosures to new, but still barren, enclosures results in elevated urinary **cortisol** and increased stereotypic pacing, and although the reasons for this are unclear both can be reduced to some extent by the provision of branches and hiding places (Carlstead *et al.* 1993).
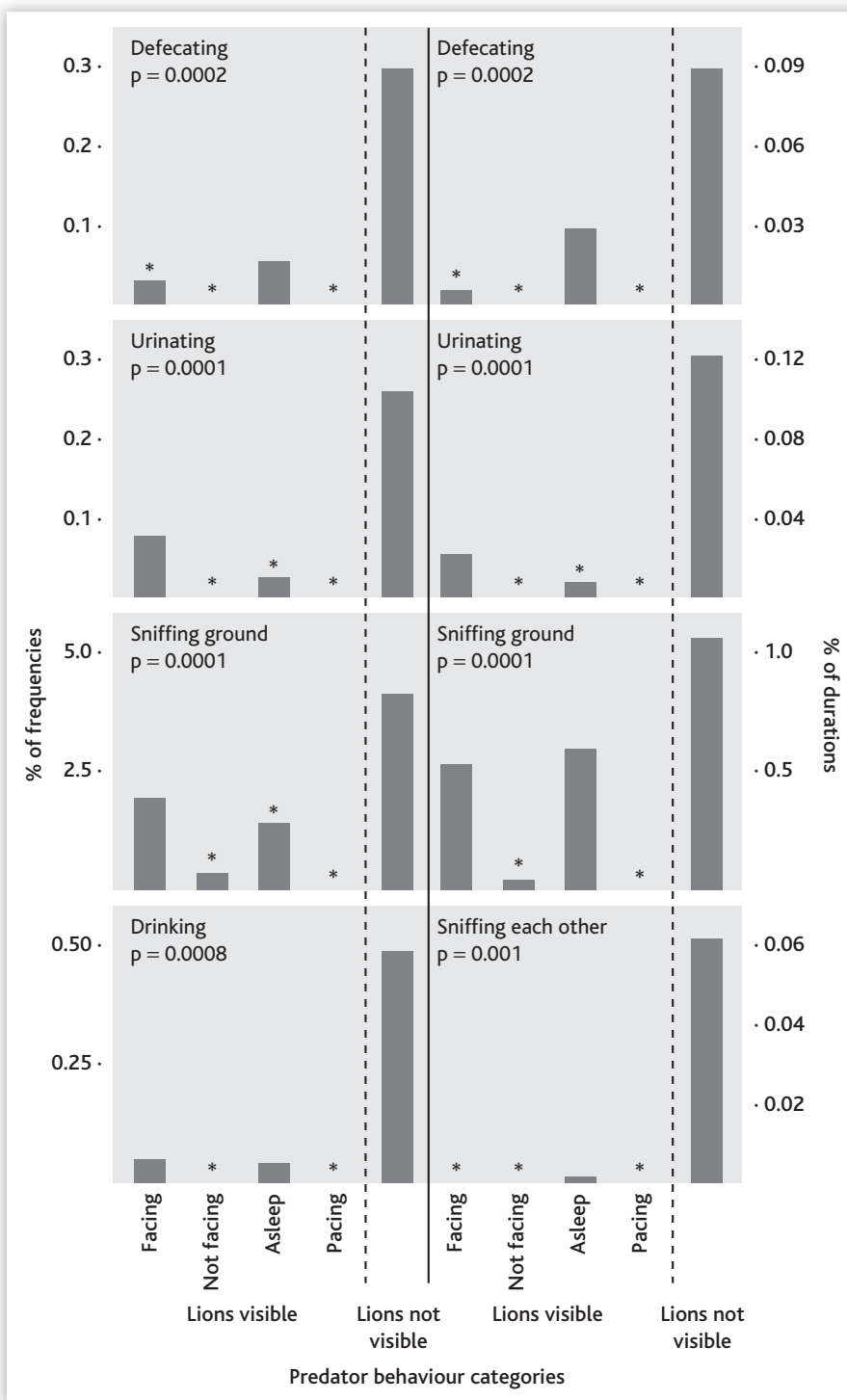
Figure 4.22 When lions were visible to ungulate species in a mixed-species African exhibit, the ungulates showed significantly less (as indicated by asterisks) defecating, urinating, sniffing the ground, drinking, and sniffing each other compared with when the lions were not visible to them. This was true even if the lions were visible but asleep, and the ungulates stopped all these behaviours if the lions were pacing. (Adapted from Stanley and Aspey 1984)
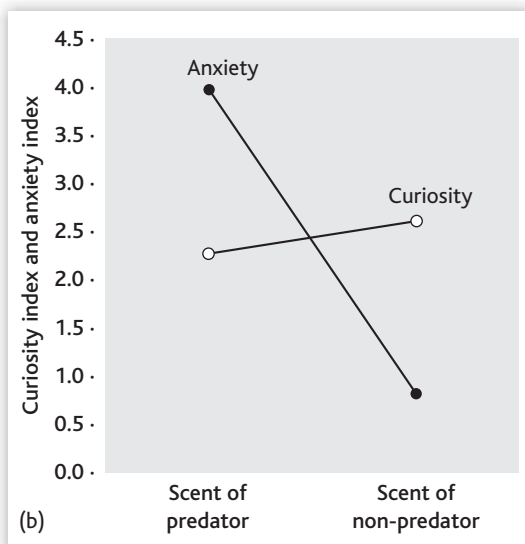
Figure 4.23 (a) Cotton-top tamarins *Saguinus oedipus* are slightly more curious about non-predator faecal scents than those of predators, but predator scents make them behave with higher anxiety. (b) The curiosity and anxiety indices are the totals of several individual behaviours in each of those categories. ((a) Photograph: Hannah Buchanan-Smith; (b) Adapted from Buchanan-Smith *et al.* 1993)

The adverse effects of translocation in this last study may well be a feature of non-naturalistic enclosures. Indeed, regular routine alternation of two gorilla groups between two naturalistic enclosures at Zoo Atlanta has been used as a form of enrichment for the animals (Lukas *et al.* 2003). The evidence to support this is that the animals show increased feeding and use of the enclosure, and less **self-directed behaviour**, after being moved to the other enclosure. This sort of manipulation has been used elsewhere for the routine movement

of other species (including tapirs *Tapirus indicus*, tigers, and babirusa *Babyrousa babyrussa*, as well as primates) between exhibits (White *et al.* 2003), and results in changes in the activity of the animals.

With the increasing trend towards naturalistic enclosures in zoos, a number of opportunities have arisen to monitor behavioural change when animals (again, mostly primates) are moved from traditional cages to naturalistic enclosures and, in some cases, to free range. As expected, the changes seen are usually interpretable as beneficial in terms of producing more wild-type behaviours. For example, the transfer of a group of Hanuman langurs *Semnopithecus entellus* at London Zoo from a traditional cage to a naturalistic enclosure led to an increase in eating and locomotion, and a decrease in dozing, allogrooming, and aggression (Little and Sommer 2002) (**Fig. 4.24**).

How do we interpret this? At face value, it looks as though there has been a positive change in the behaviour of the animals, but the authors caution us that the animals' activity budgets in both old and new enclosures were within the ranges seen in these animals in the wild (see **section 4.5**). Even less clear are the results shown in a study of a gorilla at San Francisco Zoo moved from an old-style concrete grotto to a new naturalistic enclosure (Goerke *et al.* 1987). In the new enclosure, the gorilla showed less **coprophagy** and **regurgitation/reingestion** (see **section 4.4**), but more self-clasping (**Fig. 4.25**) and less play. A similar transfer of both gorillas and chimps at Lincoln Park Zoo, Chicago, led to decreased attention and increased inactivity in both species and an extended period of adjustment (Ross *et al.* 2011).

Changes in group composition

Changes in group membership can occur because of introductions of new animals to, or removals of animals from, established groups, through the setting up of new groups, or through births and deaths. Again, much of the literature on introductions either concerns laboratory primates (e.g. Scruton and Herbert 1972; Williams and Abee 1988; Brent *et al.* 1997; Seres *et al.* 2001) or consists of descriptive accounts of successful
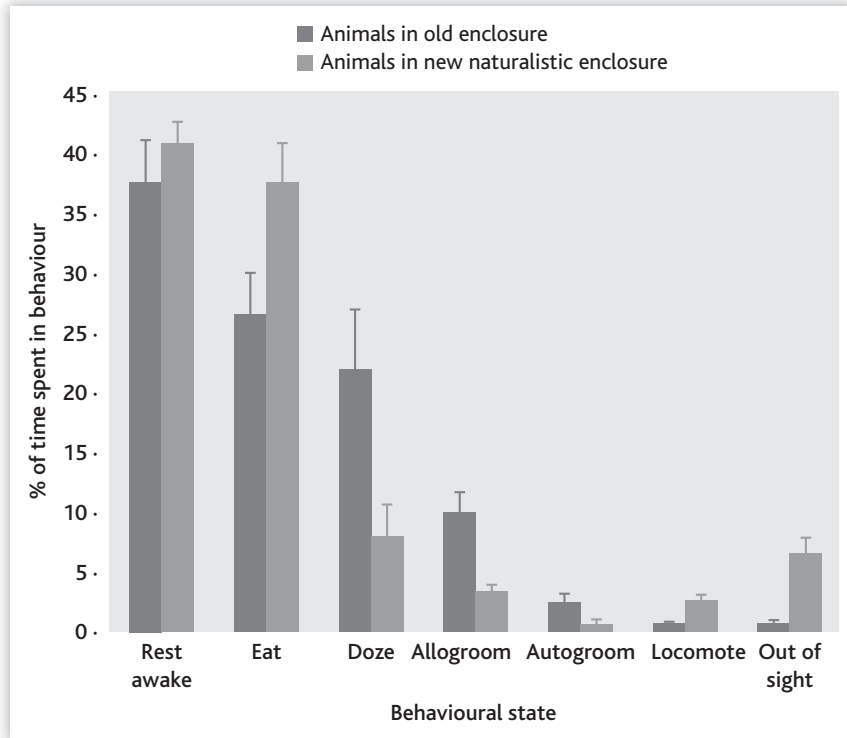
Figure 4.24 Hanuman langurs *Semnopithecus entellus* show changes in their behaviour consistent with enrichment when they are moved from old traditional-style accommodation to a new naturalistic enclosure, but, in fact, neither is outside the range of behaviours that these monkeys show in the wild. (Adapted from Little and Sommer 2002)
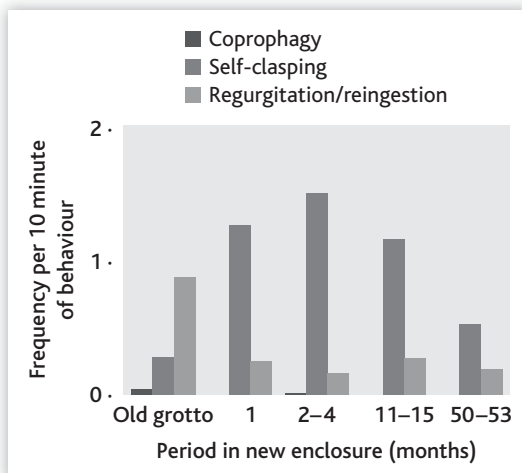
Figure 4.25 When a juvenile gorilla was moved from an old-style concrete grotto to a new naturalistic enclosure, some stress-related behaviours declined (coprophagy and regurgitation/reingestion) while another one (self-clasping) increased. This shows how difficult it can sometimes be to interpret changes in behaviour. (Adapted from Goerke *et al.* 1987)

procedures (e.g. Mayor 1984; Thomas *et al.* 1986; Hamburger 1988). Studies with quantitative data are less numerous.

The following are some examples to show the range of situations in which introductions may occur in zoos.

• Male maned wolves *Chrysocyon brachyurus* at Houston Zoo and Fossil Rim Wildlife Center, both in Texas, were removed from their mates while the latter were giving birth. Later, they were reintroduced in stages, at the end of which they had contact with, and showed affiliative behaviours towards, the pups (**Fig. 4.26**) (Bestelmeyer 1999). Three female Asian elephants *Elephas maximus* were introduced into an established group at a different zoo; two of them showed increased stereotypies and the other showed decreased stereotypies, which eventually returned almost to pre-introduction

(a)

(b)
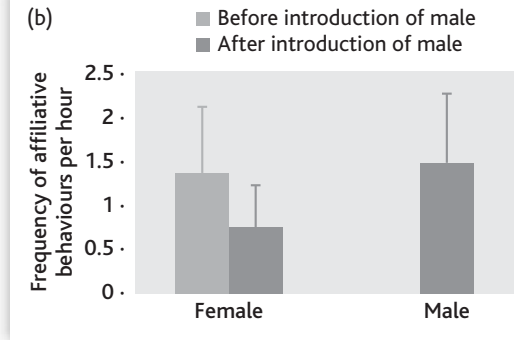
Figure 4.26 (a) Maned wolf *Chrysocyon brachyurus*. (b) Male maned wolves introduced gradually to their 7–12-week-old pups show affiliative (friendly) behaviours towards them. ((a) Photograph: Ray Wiltshire; (b) From Bestelmeyer 1999)

levels. The elephants in the established group showed increased social and manipulation/exploration behaviours (Schmid *et al.* 2001).

• Five hand-reared infant gorillas were introduced into an established group at Bronx Zoo. The infants showed strong tendencies to associate with other infants, but also with the silverback male (McCann and Rothman 1999).

What happens when animals are removed from groups?

• When two adult Campbell's monkeys *Cercopithecus campbelli* were removed from a laboratory-housed group, there was an increase in social interactions and play in the remaining animals, but they directed more aggression to remaining members of the matriline—that is, the group of direct female descendents of a particular mother—from which the females had been removed (Lemasson *et al.* 2005).

• Removal of a male giraffe *Giraffa camelopardalis* at Atlanta Zoo was followed by increased activity, stereotypies, and contact behaviours, and reduced utilization of the enclosure by the remaining two females (Tarou *et al.* 2000).

• When an elderly female chimpanzee died at Edinburgh Zoo, other members of the group were seen to groom her in the time immediately before death, but not after, and a young male member of the group subsequently attacked the corpse three times (Anderson *et al.* 2010). After the death of her mother at Dublin Zoo, an infant orang-utan associated more with a related adult female (Whilde and Marples 2011).

Regardless of any welfare considerations, studies such as these can indicate to us something about the social dynamics of species in relation to which detailed field studies are lacking.

4.3.4 What do these examples tell us?

Reading through the previous three sections may leave us feeling that there is no overall answer to the question 'How does the zoo environment

affect behaviour?', and that the answer depends on which species, which behaviour, and which aspect of the zoo environment we are considering. This is probably a valid conclusion and, given the diversity of animal life histories and adaptability, we should be surprised if this were not the case.

However, there are some general points that we can make. The first is that the zoo environment is, indeed, made up of a lot of different variables that may influence behaviour in different ways. So we may, for example, be interested in how enclosure size affects behaviour, but we must recognize that groups in larger enclosures may be made up of more animals and therefore may compete more for the food that is provided, but may also be able to hide better from each other. So, in this situation, would we expect a behaviour such as aggression to increase, decrease, or stay the same? This is not an easy prediction to make, but it is the sort of approach that we must take if we are to make sense of the zoo environment and how animals adjust to it.

A second general point is that many animals in zoos do, indeed, appear to have sufficient behavioural flexibility to be able to adjust to the conditions imposed on them by the variables of the zoo environment. This may be because the range of environmental variability to which those species are adapted in the wild is as great as, or greater than, the variability of the zoo environment; alternatively, it may be that modern zoo environments are not actually all that different from wild environments. Perhaps, it is a bit of both.

Either way, this brings us to two related issues that we will consider in the rest of this chapter.

1. How would we know if the zoo environment was outside the range of variability that the animal could accommodate? One possible indicator of an animal's difficulty in coping with its environment is the appearance of abnormal behaviours, which we will consider in the next section, and again in **Chapter 7**.

2. How do we know that the behaviours we are seeing are within the animal's normal range of flexibility? One way is to look at behaviour in the wild, and we will consider this in **section 4.5**.

4.4 Abnormal behaviours

It has been known for a long time that captive animals sometimes show behaviours that, to us, look unusual and pointless enough for us to label them 'abnormal'. Such behaviours are well known in agricultural animals, among which examples include pacing, weaving, rocking, head-shaking, bar-biting, self-mutilation, feather-pecking, tail-biting, inadequate sexual or parental behaviour, inactivity, hyperactivity, and other apparently odd behaviours (Fraser and Broom 1990). Examples of these behaviours used to be well known in the zoo world as well, and early descriptions of numerous examples are given by Morris (1964) and Meyer-Holzapfel (1968). The sorts of behaviour that they described included abnormal aggressiveness, stereotyped movements (straight, circular, and figure-of-eight patterns), self-mutilation, and others.

Since those studies, much effort has gone into trying to establish the underlying causes of these behaviours, investigating whether they necessarily constitute a welfare problem and how best to deal with them. Fortunately, with improvements in housing and husbandry, abnormal behaviours are less of a problem in zoo animals than they were a few decades ago.

4.4.1 What is 'abnormal behaviour'?

What exactly do we mean when we label a behaviour as 'abnormal'? Meyer-Holzapfel (1968) viewed abnormal behaviours as those that were '*uncommon or even absent in **free-ranging** animals*'. A later review used the term to denote that the behaviour was in some way **pathological** (Erwin and Deni 1979). Mason (1991) has pointed out that there are two senses in which the term 'abnormal behaviour' is used:

- it is rare or unusual;
- it is apparently lacking in function and may be harmful to the animal, possibly as a consequence of some underlying pathology.
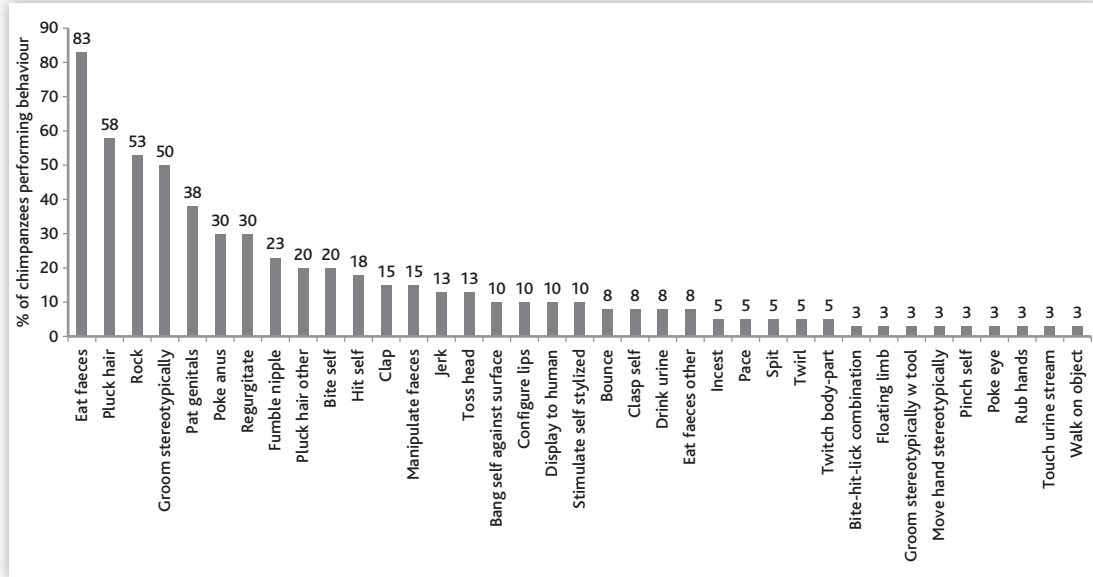
Figure 4.27 Apparently abnormal behaviours shown by a multi-zoo sample of zoo chimpanzees. The most common was 'eating faeces' (83%), but this is also observed in wild chimpanzees. (From Birkett and Newton-Fisher 2011/CC-BY)

She also points out that, even if a behaviour is seen as abnormal in the first of these senses, it does not necessarily mean that it is also abnormal in the second sense. It is best to use the term, if at all, in a relative rather than an absolute sense, particularly if it is being used to refer to a 'rare' behaviour—rare compared with what? 'Compared with the wild' is a commonly used criterion, on the grounds that these behaviours are not usually seen in wild populations, but we must be careful in applying this criterion as apparently abnormal behaviours are seen in the wild. For example, L.J. Miller *et al.* (2011a) describe what looks very like stereotypic swimming in wild lemon sharks *Negaprion brevirostris*, and their suggested causal factor (pre-feeding anticipation) may also be one of the factors that is linked with stereotypies in a zoo context. (See **section 4.5** for more on wild–captive comparisons.)

Even if a behaviour is not often seen in the wild, it may nevertheless be relatively common in captivity and may not be linked with serious health issues for the animal. A recent study of zoo chimpanzees, for example, concluded that all the animals surveyed showed at least one abnormal behaviour (Birkett and Newton-Fisher 2011), although it is by no means clear that all the behaviours included would be considered abnormal by many people. For example, the most common 'abnormal' behaviour seen was 'eating faeces' (**Fig. 4.27**). But this is also seen in wild chimps (Payne *et al.* 2008), so it is by no means obvious that this should be regarded as abnormal. Increasingly, some such behaviours are now being referred to as 'undesirable' rather than 'abnormal'. An example of this is regurgitation and reingestion in gorillas (Lukas 1999)—that is, when the animals bring food voluntarily (not reflexly, as in vomiting) back up from the stomach to the mouth or a substrate, and then reingest it (**Fig. 4.28**). This behaviour is shown by 65 per cent of captive gorillas and occupies substantial proportions of their activity budgets, and hence, in a relative sense, is 'normal' for captive gorillas (Lukas 1999). It is possible that this behaviour is performed instead of spending time feeding and it is unclear whether it reflects poor welfare, although the fact that the regurgitated food has high acidity suggests that it does have negative welfare consequences
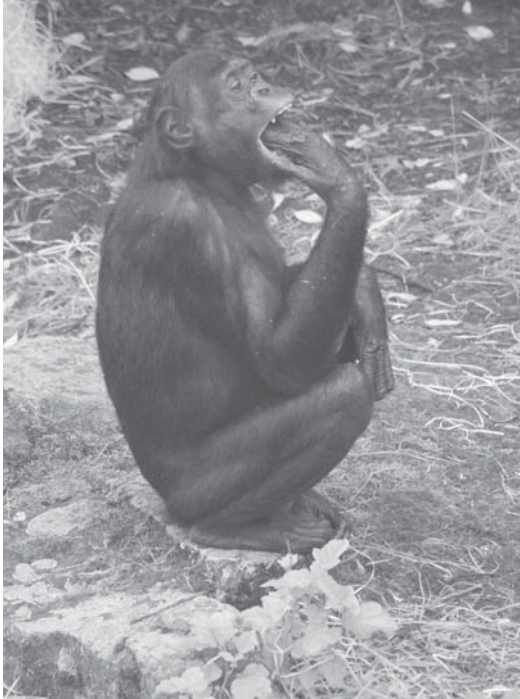
Figure 4.28 Regurgitation/reingestion in a bonobo *Pan paniscus*, who is putting her hand in her mouth to stimulate regurgitation. (Photograph: Jeroen Stevens)

Figure 4.29 Feather-plucking has been well documented in an agricultural context and is sometimes also seen in zoo-housed birds such as this rose-ringed parakeet *Psittacula krameri*. (Photograph: Dennis Appels)

(Hill 2009). Therefore using the term 'undesirable' can avoid some of the negative assumptions that accompany the term 'abnormal', though we should not then assume that the behaviour is more acceptable.

The term 'abnormal behaviour' in the zoo context covers a number of apparently different kinds of behaviour, which are generally seen as responses to some aspect of the captive environment. Meyer-Holzapfel (1968) lists the following:

- abnormal escape reactions, aggressiveness, sexual behaviour, mother–infant relations;
- refusal of food;
- stereotyped motor reactions;
- self-mutilation (**Fig. 4.29**); perversion of appetite;
- apathy;
- prolonged infantile behaviour and regression.

Erwin and Deni (1979) distinguish those abnormal behaviours that are 'qualitative'—that is, different in form (for example, stereotypies, self-biting)—from those that are 'quantitative'—that is, when the animal shows elevated or depressed levels of a behaviour that is otherwise normal (for example, hyper-aggression, inactivity).

Many of these behaviours are no longer seen as significant problems for zoos, partly because zoo environments are now much better at meeting the needs of the animals and partly because our knowledge of the extent to which animals show the behaviour has improved. As an example, we can consider **self-injurious behaviour (SIB)**, sometimes referred to as 'self-mutilation'. Primates have traditionally been seen as particularly susceptible to this, and some laboratory colonies, particularly of rhesus monkeys, show high rates of self-injury (Novak 2003). But a survey of British and Irish zoos by Hosey and Skyner (2007) revealed that,

while self-injury was found in a wide **taxonomic** range of primates in zoos, it was nevertheless very rare, with only twenty-four animals being reported as showing this over a period of about 15 years, although it should noted that these data are from self-reports from the zoos.

4.4.2 Abnormal behaviour and welfare

The presence of abnormal behaviours is often taken uncritically to indicate that the animal is suffering in some way or that its welfare is, or has been, compromised. This topic is explored further in **Chapter 7**, but at this point we can say that abnormal behaviours show such diversity of form, as well as of motivational, physiological, developmental, and environmental correlates, that each probably has to be considered separately. In the case of stereotypies, for example, there is clearly a link with welfare, but it is not clear what that link is. Mason and Latham (2004) discuss several possibilities, including that the animal is 'self-enriching', or that repetition of the behaviour helps the animal to improve its own welfare. In the end, it is safest to assume, at least for stereotypy, that its presence indicates that the animal has been subjected to a suboptimal environment at some stage in its life.

4.4.3 Stereotypies

Stereotypies have probably been of more concern in the zoo context than most other kinds of abnormal behaviour, simply because they are so obvious when present and they cause anxiety in zoo visitors who see them. However, most of what we know about their underlying causes is derived from the laboratory and agricultural literature (**Fig. 4.30**).

Stereotypies can be characterized as behaviour patterns that are repetitive and invariant (Mason and Rushen 2006). They are often seen

Figure 4.30 An example of a stereotypy is bar-biting, which is illustrated here in a stabled horse. (Photograph: Georgia Mason)

in environments that appear to be poor for the welfare of the animal, although sometimes they persist in high-quality environments, thus indicating only that the animal has been exposed to a poor environment in its past (Mason 1991). Often, they are associated with lack of stimulation or with stressful events; stereotypic behaviour may represent the animal's attempts to cope with its environment, but the evidence for this is not as clear as we would wish (Rushen 1993; Broom 1998; Mason and Latham 2004).

Research has indicated a possible link between stereotypies and **perseveration**, which would suggest that stereotyping animals are unable to inhibit elicited behaviours (Garner and Mason 2002; Vickery and Mason 2005). This would imply that the captive environments that produce stereotypies do so by affecting the way that brain structures (such as the striatum[15]) organize behaviour. This approach may offer ways of explaining why some animals appear to be more prone to developing stereotypies than others.

More recently, Mason (2006) has suggested defining stereotypies as '*repetitive behaviours induced by frustration, repeated attempts to cope and/or CNS dysfunction*',[16] a definition that puts more

[15] The striatum is a part of the basal ganglia, which are masses of grey matter (i.e. neurons or nerve cells) deep within the brain, and appears to have a role in the coordination of locomotion.

[16] CNS is an acronym for the central nervous system, which comprises the brain and the spinal cord.

emphasis on possible causal factors than it does on what the behaviour looks like. She sees the first of these (induced by frustration, attempts to cope) as the maladaptive, but reversible, responses of normal animals to abnormal environments, while the second (CNS dysfunction) implies abnormal animals. In zoo animals, however, the cause of a stereotypy is often not known, and Mason *et al.* (2007) suggest using the term 'abnormal repetitive behaviours (ARBs)' for such behaviours.

In zoo animals, stereotypies may manifest themselves as pacing (for example, in bears (Wechsler 1991; Montaudouin and Le Pape 2005)), swaying (for example, in elephants (Wilson *et al.* 2004)), oral stereotypies (such as licking in **giraffids** (Bashaw *et al.* 2001) (**Fig. 1.7**)), and other kinds of repetitive movement (**Fig. 4.31**). Several studies have looked for possible correlates of these behaviours within the zoo environment. A study of primates at St Louis Zoo indicated that rearing history (particularly hand-rearing) was more important in eliciting stereotypies than any of the measured variables of the animals' current housing (Marriner and Drickamer 1994). A similar conclusion, that early social and environmental deprivation was implicated in the development of abnormal behaviour, was reached by Mallapur and Choudhury (2003) in a survey of eleven species of primate across ten different Indian zoos, and by Martin (2002) in a study of resocialized chimpanzees in British zoos. Indeed, there is now ample evidence of the link between maternal deprivation and stereotypic behaviours (Latham and Mason 2008).

But current housing variables can also be important. For example, a survey of nine felid species in eleven different enclosures at Edinburgh Zoo found that, although stereotypic pacing tended to occur at enclosure edges, larger enclosures were not associated with higher levels of pacing; however, not being fed on alternate days did result in pacing on the non-feed days (Lyons *et al.* 1997).

Figure 4.31 Characteristic 'figure-of-eight' pathway caused by repetitive pacing, as in this dhole *Cuon alpinus*. (Photograph: Geoff Hosey)

Social factors also play a part: paired tigers showed more stereotyped pacing when housed near neighbouring tigers than when not (De Rouck *et al.* 2005) (see **Table 4.3**). It also seems to be the case that some kinds of animal are more prone to developing stereotypies than others, or may be prone to developing particular kinds of stereotypies. Ungulates, for example, are at particular risk of developing oral stereotypies, and this seems to be related to deficiencies in captive feeds (Bergeron *et al.* 2006). Carnivores, on the other hand, often show locomotory stereotypies ('pacing') which may represent frustrated attempts to escape, because the frequency of stereotypies correlates with natural home range size (Clubb and Vickery 2006) (see also **Box 4.4**).

Box 4.4 **STEREOTYPY AND CARNIVORES: WHY ARE SOME SPECIES WORSE THAN OTHERS?**

We can illustrate our increased understanding of stereotypies by looking at a specific example—the Carnivores. It has long been known that Carnivores seem to be particularly prone to developing stereotypies. Bears, for example, often show pacing (locomotory stereotypy) and may also show high rates of begging (**Fig. 4.32**). In a survey of fifty-eight zoos, Van Keulen-Kromhout (1978) found that high levels of stereotypy and begging were found in the three species for which she had sufficient data: polar bears *Ursus maritimus*, brown bears *U. arctos*, and Himalayan black bears

Figure 4.32 Bears often perform unusual behaviours in captivity. (Photograph: Vicky Melfi)

U.thibetanus. She also noted that begging was inversely related to stereotypy, and that polar and Himalayan bears showed more stereotypy than browns, but that browns showed more begging.

Later descriptions of stereotypies in bears concentrated on more detailed observations and attempted to correlate the behaviour with underlying motivations. Wechsler (1991) analysed polar bear locomotory stereotypies and suggested that they develop from frustrated appetitive (for example, food-seeking, food-handling) behaviours. Montauduoin and Le Pape (2004) linked stereotypic walking in brown bears to the chance of obtaining food. And Vickery and Mason (2004) considered that stereotypies were more food-related in sun bears *Helarctos malayanus* than in black bears. Thus, the evidence seems to indicate that stereotypies may develop when animals are prevented from performing behaviours that they are adapted to show in the wild.

This possibility has been explored more fully in carnivorous mammals by Clubb and Mason (2003, 2007) who, after controlling for **phylogeny** (i.e. the likelihood that some correlations will appear in closely related species because of common evolutionary descent), found that the amount of stereotypic pacing that these animals show in captivity can be predicted from their home range size in the wild (**Fig. 4.33**).

Note that polar bears (PB in **Fig. 4.33**) seem to fare particularly badly, presumably because their home ranges in the wild are so vast that even the most generous zoo enclosure cannot replicate them. This result implies that Carnivore stereotypies are not the result of thwarted foraging or hunting behaviours, but are better interpreted as frustrated attempts to escape (Clubb and Vickery 2006). As far as zoos are concerned, the message might be that better design of Carnivore enclosures is needed to facilitate the animals in performing more of their naturalistic behaviours. Another conclusion may be that there are some species that are unsuitable for keeping in zoos.

This method of comparative analysis, described in more detail by Clubb and Mason (2004), offers promise for giving further insights into the ways in which captive environments affect different species in different ways and, hopefully, will be applied to other taxa as the required data become available. Indeed, Mason (2010) has noted that in many cases we can divide species into those with relatively good and those with relatively poor captive welfare, and examples of both can often be found in the same taxonomic group, suggesting that the differences are due to ecological and life history variables rather than what species they are. Comparative analyses, using these ecological variables, offer a possible way of predicting how species will respond to captivity.
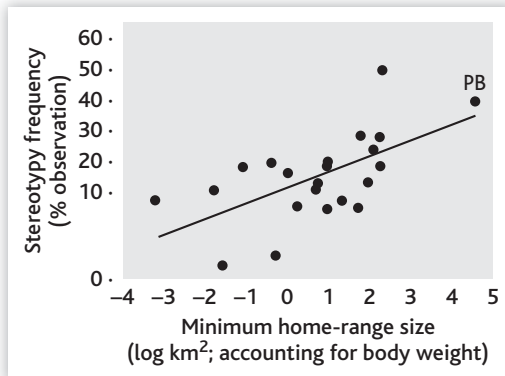
Figure 4.33 Frequency of stereotypy seen in a number of species of Carnivora plotted against the logarithm of their home range size, with correction for body weight (because bigger animals have a bigger home range). The polar bear *Ursus maritimus* is labelled PB. (Adapted from Clubb and Mason 2003)

What does all this mean in terms of the management of zoo animals? More than four decades ago, Boorer (1972) concluded that stereotypies were probably not a serious problem, but that they should be dealt with by the zoo because they do not portray the best image of the animals for the visiting public. While the second part of that statement is undoubtedly true, we now know much more about stereotypies and we are now very aware that they might indicate that the animal is in a situation that represents poor welfare. Efforts to deal with stereotypies in zoo animals range from attempts to prevent their development, to trying to stop them (a common method

with agricultural animals), to providing some sort of enrichment to reduce them. Judging by the agricultural literature, trying to stop an animal from performing stereotypies is unlikely to work and could result in even worse welfare (Mason 1991). Giraffes do not reduce their stereotypic licking when a bitter-tasting chemical is applied to the substrates that they lick; they just lick elsewhere (Tarou *et al.* 2003). However, increasing dietary fibre (Baxter and Plowman 2001), or using enrichments that require more tongue manipulation by the animals (Fernandez *et al.* 2008), can result in a decrease in oral stereotypies in giraffes. Other ways of attempting to stop stereotypies include training (Coleman and Maier 2010; Shyne and Block 2010), but see **Box 13.4**, and housing manipulations, such as erecting visual barriers (Bashaw *et al* 2007) although this did not reduce stereotypies in tigers.

Providing some sort of enrichment (see **Chapter 8**) is a common way of attempting to reduce the amount of stereotypies that zoo animals show, as the following examples demonstrate.

- Two Amur tigers *Panthera tigris altaica* at Zurich Zoo were provided with feeding boxes that had to be actively opened by the animals (Saskia and Schmid 2002). Stereotypic pacing reduced in the female when the boxes were present, both when she was alone and when paired with the male, and also reduced for the male when he was paired with the female.
- In another study, stereotypic behaviours decreased in a female leopard when she was trained to pursue bird sounds, leading to bird parts on a feeder belt (Markowitz *et al.* 1995).

So how effective is environmental enrichment in reducing stereotypies? Reviews of the literature by Swaisgood and Shepherdson (2005, 2006) have shown that enrichment is, indeed, a suitable technique for this, and is associated with significant reductions in stereotypy about 53 per cent of the time. However, they found that, in many cases, the form of enrichment was tailored to the particular needs of individual animals. This, and methodological issues to do with sample size, experimental design, and analysis, meant that little in terms of general conclusions about the effectiveness of different treatments could be drawn from the studies (there is more on this topic in **Chapter 8**).

4.4.4 Birds, reptiles, amphibians, and fish

Up to now, all our examples of abnormal behaviour have been mammalian. This is not because other animals do not show abnormal behaviour, but rather because there are fewer studies on them in zoos. However, studies on birds do show many similarities to the general picture outlined above in relation to mammalian examples. Parrots, in particular, are liable to develop locomotory and oral stereotypies, which may well have the same underlying mechanisms as mammalian stereotypies (Garner *et al.* 2003). These also can be reduced by appropriate environmental enrichment, such as pair, rather than single, housing (Meehan *et al.* 2003), and by adding enrichments to promote feeding and locomotion (Meehan *et al.* 2004).

Again, rearing can affect the development of stereotypies: Hawaiian crows *Corvus hawaiiensis* show higher rates of stereotypy if isolate-reared compared with socially reared (Harvey *et al.* 2002).

Another kind of abnormal behaviour that has been reported in parrots is self-inflicted feather-pecking, which appears to have different environmental and genetic correlates from stereotypy (Garner *et al.* 2006) but, at least in crimson-bellied conures *Pyrrhura perlata*, does not appear to be reduced by environmental enrichment (Van Hoek and King 1997).

Even less has been written about abnormal behaviours in reptiles and fish (and apparently nothing on amphibians). Reptiles are commonly perceived, probably erroneously, as being very adaptable to captive conditions (Warwick 1990); in addition, they are often regarded as having less behavioural complexity and lower rates of activity than birds and mammals. Nevertheless, they do show behavioural changes in captivity that appear to be responses to stress. Some of these have been

described by Warwick (1990) and they appear to be of two sorts:

- mobile activities (such as hyperactivity and interactions with transparent boundaries), which perhaps represent attempts to escape (**Fig. 4.34**);
- hypoactivity/lethargy and anorexia, which perhaps are strategies to 'wait out' the stressful conditions.

Whether these can become stereotypies in the sense described above, and how equivalent they are to abnormal behaviours seen in mammals and birds, is unclear.

Finally, turning to fish, there has been recent discussion about exactly what welfare concerns we should have (Chandroo *et al.* 2004; Conte 2004; Ashley 2007), and behavioural indicators of stress are not clear. Evidence from the **aquaculture** industry suggests that welfare issues for fish can arise from transportation, handling, and inappropriate stocking densities (Ashley 2007), so we should be aware of these in the zoo and aquarium context as well. Possible stereotypies in fish include vertical swimming patterns in Atlantic halibut *Hippoglossus hippoglossus* at high stocking densities, and surface-breaking behaviour in rays in public aquariums (Ashley 2007) (**Fig. 4.35**). Surface-breaking behaviour in these fish appears to be related to foraging (Scott *et al.* 1999a) and can be reduced through feeding enrichment (Scott *et al.* 1999b). There is evidence that captive environments may bring about an increase

Figure 4.34 Emerald tree monitor *Varanus prasinus* interacting with a transparent boundary, which may be consequence of stress (Photograph: Geoff Hosey)

Figure 4.35 Surface swimming in a thornback ray *Raja clavata*. This may be a form of stereotypy and is seen in other ray species as well. (Photograph: Geoff Hosey)

in aggression in some fish (Kelley and Magurran 2006), but, in general, how the zoo or aquarium environment affects fish behaviour is unknown.

4.5 Comparison with the wild

At one time, the cages and enclosures used to house zoo animals were predominantly concrete and bars. These bore no resemblance to the natural environment of the animals, and the incidence of abnormal behaviour was testament to the difficulty that animals had in coping with these environments. A move towards more naturalistic environments in zoos in the latter part of the twentieth century helped to bring the zoo environment more within the range of environments in which the animals' behaviours were able to operate (see **Chapter 2**). These developments were, at first, based on perceptions of what made a good captive environment from a human point of view, but gradually became more informed by the growing amount of knowledge of what animals did in the wild (Redshaw and Mallinson 1991).

This aspect of zoo biology is dealt with in more detail in **Chapter 6**, on 'Housing and husbandry', **Chapter 7**, on 'Animal welfare', and **Chapter 8**, on 'Enrichment'. This section deals with what may be a logical consequence of this philosophy: that behaviour in the wild can be used as some sort of standard with which to compare behaviour in the zoo (see **Box 4.5**). Just what sort of standard we will consider later but, first, we will establish some cautions about how to interpret such comparisons.

Box 4.5 COMPARING BEHAVIOUR IN THE ZOO WITH BEHAVIOUR IN THE WILD

There are a number of examples in the literature of comparisons of behaviour in the zoo with behaviour in the wild. The two examples given here (hopefully) reflect the differing approaches that researchers have taken to this area of study. (A further example is given in **section 8.3.1.**)

Höhn *et al.* (2000) compared the activity budgets and agonistic behaviour of Eastern grey

kangaroos *Macropus giganteus* (**Fig. 4.36a**) at Neuwied Zoo in Germany with those shown in the wild in Australia. The same observers collected data in the same way and with the same behavioural measures in the two locations. The group sizes of the animals were similar (56 animals in the zoo group; 50–60 in the wild group) and the zoo enclosure was a naturalistic one that resembled the wild.
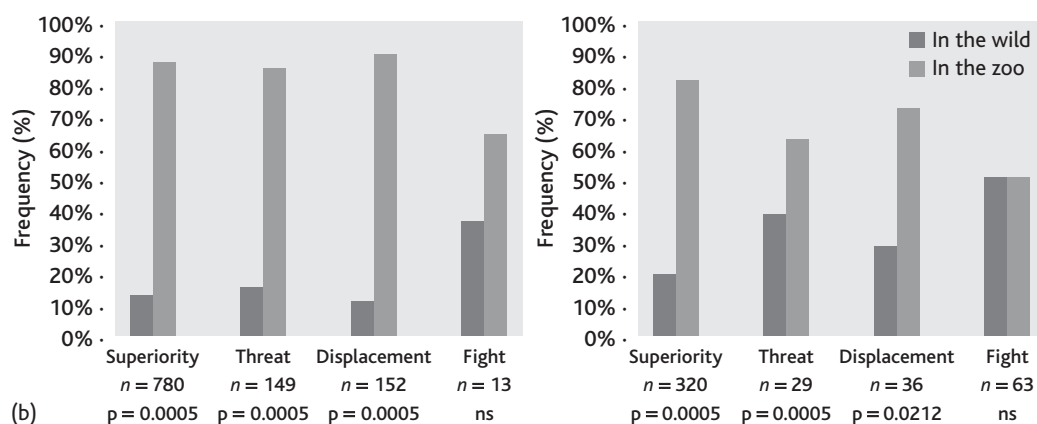
Figure 4.36 (a) Eastern grey kangaroo *Macropus giganteus*. (b) Frequencies of different aggressive behaviours (expressed as percentages) of large (left graph) and medium-sized (right graph) male Eastern grey kangaroos in the wild and in a zoo. The zoo animals show more low-level aggression (superiority, threat, displacement), but not high-level aggression (fight), compared with those in the wild. ns, not significant. ((a) Photograph: Geoff Hosey; (b) Adapted from Höhn *et al.* 2000)

The observers found that the activity budgets of the animals in the two situations were not particularly different, although there were some differences in some behaviours. Agonistic behaviour was consistently more frequent in the zoo kangaroos in three of the four measures of agonistic behaviour (**Fig. 4.36b**). However, escalated aggression was not more frequent, which suggested that the animals were using lower-intensity aggression more often to avoid damaging conflicts.

Our second example comes from a study by Kerridge (2005) on the activity budgets of black-and-white ruffed lemurs *Varecia variegata* (**Fig. 4.37a**). She collected data in several British zoos and in the wild in Madagascar, again using the same behavioural measures. The purpose of this was to identify whether the captive animals had different activity budgets and, if so, whether environmental enrichment could be used to make them more similar to those exhibited in the wild. The results (**Fig. 4.37b**) showed that the captive animals spent more time in grooming and social behaviour, and less time in feeding and moving, than the wild lemurs; they also used fewer different kinds of food manipulation. Environmental enrichment (providing whole rather than chopped food) had the effect of increasing the feeding times of the captive lemurs and manual manipulation of the food, but did not affect time spent in movement.

These two studies illustrate several features of wild–captive comparisons: the observers in the two situations may or may not be the same individuals; particular behaviours may be chosen for comparison, but the use of activity budgets is a common technique; and there is an assumption that other variables in the comparison do not impact significantly on the results. As a consequence, we should be careful how we interpret the results of zoo–wild comparisons.
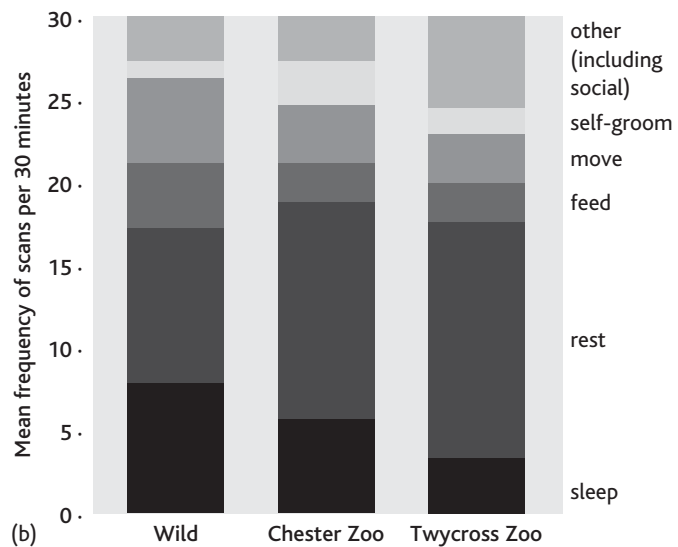
Figure 4.37 (a) Black-and-white ruffed lemur *Varecia variegata*. (b) Activity budgets for black-and-white ruffed lemurs in the wild and in two different zoos. The zoo-housed lemurs spend less time feeding and moving, and more time in grooming and social behaviour, than their wild counterparts. ((a) Photograph: Geoff Hosey; (b) Adapted from Kerridge 1996)

4.5.1 Interpreting the results

It has been noted, particularly by Veasey *et al.* (1996a), that wild–captive behavioural comparisons pose a number of methodological and technical difficulties that hamper our interpretations of what these studies show.

Veasey *et al.* (1996a) list the following:

- observers may influence the behaviour of wild-living animals more than they do those living in the zoo;

- changes in both biotic and abiotic factors[17] can bring about quantitative and qualitative changes in behaviour in the wild;

- many species are rare or extinct in the wild and in limited numbers in captivity, casting doubt on how representative the behaviour is;

- small sample sizes cause difficulties, including the need to pool data, often from different subspecies or even hybrids;

- the zoo population may itself not be representative, because of the zoo survival of animals that may be unfit to survive in the wild;

- there is considerable behavioural variation between individuals and, indeed, between populations in different zoos;

- the same behavioural measures (indeed, the same observers as well) are rarely used in comparisons.

The same authors followed up this critique with a comparison of behaviours of wild and zoo-housed giraffes to try to assess how much these methodological difficulties affected the results (Veasey *et al.* 1996b). They collected data at four different zoos in the UK, watching giraffes in their paddocks in the day and in their sleeping quarters at night, and also collected data on wild giraffes in Zimbabwe using four different data collection methods. They found that the giraffes in the four different zoos only differed from each other significantly in one behaviour—the proportion of time spent lying down (**Fig. 4.38**).

The four different data collection methods used on the wild giraffes gave significantly different results and, when the results of one of the methods were compared with one of the zoo samples, it was found that the zoo giraffes spent less time feeding and also differed from the wild giraffes in several other behaviours. The authors also suggested that the lack of significant differences between zoos was probably a consequence of small sample sizes, rather than a real lack of difference. Clearly, then, comparisons between wild and captive behaviour should attend to these technical difficulties if they are to give an answer in which we can have confidence.

4.5.2 The purpose of wild–captive comparisons

We mentioned earlier that behaviour in the wild is used as a kind of standard against which behaviour in the zoo can be compared, without saying what that standard is. In a lot of comparisons, the assumed standard is one of best welfare and the implication is that, where zoo animals differ from their wild counterparts, that difference should be interpreted as lower or impaired welfare in the zoo. This idea occurs in the literature on the welfare of farm animals, in which a number of authors have suggested that the wild ancestors of farm animals provide the standard against which to measure the welfare of the captive animals (e.g. Fraser and Broom 1990) and has become acceptable in the zoo world as well (see Lindburg 1988).

However, using welfare as the assumed standard has also been criticized by Veasey *et al.* (1996a), because it assumes that the mere expression of a behaviour improves welfare or, conversely, that not being able to do it decreases welfare, and it is by no means clear that this is actually the case. It is

---

[17] Biotic factors are those to do with living organisms (such as interactions with other animals and plants), whereas abiotic factors are those to do with non-living (physical and chemical) processes in the environment (such as light, temperature, climate).
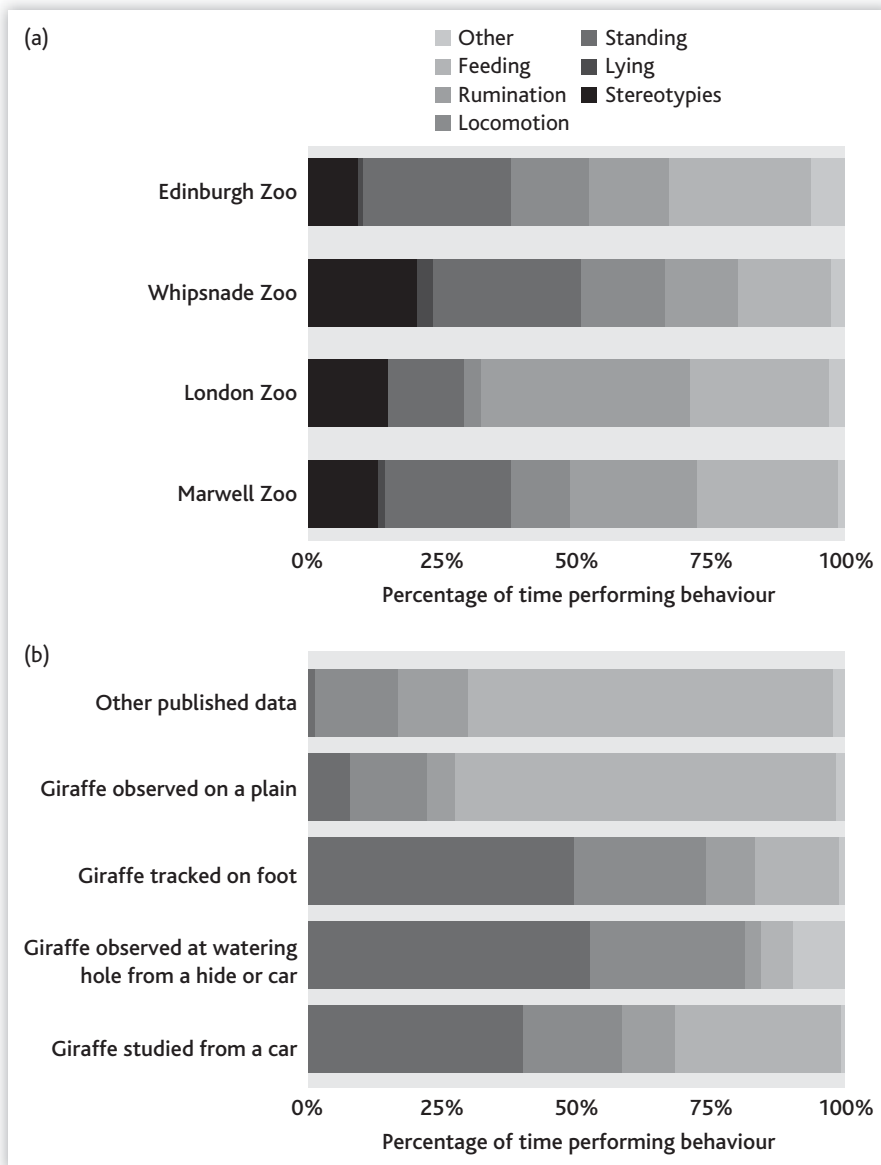
Figure 4.38 (a) Comparison of daytime activity budgets of giraffes in their paddocks at four different zoos. Although there appear to be differences, in fact only lying is significantly different between the four zoos. (b) Comparison of activity budgets for wild giraffes obtained from five different observation methods. The methods give very different results and are also different from the results for the zoo giraffes. (Both figures adapted from Veasey *et al.* 1996b)

also an assumption that the welfare of wild-living animals is the best that it can be—and this, again, may not be true (see **section 7.2.3**).

All of this is not to say that the zoo–wild comparison is of no value in our evaluations of the welfare of zoo animals; only that we should be cautious in making inferences from our comparisons. An alternative use of wild behaviour as a comparative standard is in the area of conservation. If we are concerned that zoo animals should maintain their species-typical behaviours, which is particularly the case if some of them are ultimately destined to be returned to the wild, then how conspecifics behave in the wild is a

reasonable guide to what they ought to be capable of doing. Note, however, that the methodological difficulties are still there and should be addressed in any comparison. There is also a potential difficulty of interpretation, in that it is not always clear exactly what we mean by 'wild'.

4.5.3 What is 'the wild'?

While the question of what exactly is 'the wild' may, at first sight, be as absurd a question as 'what is a zoo?', which we came across in **Chapter 1**, it is an important question to try to answer, because human activity nowadays has changed many natural environments that wild-living animals inhabit.

As an example of how these different environments affect behaviour, we can consider a study by Chang *et al.* (1999) of zoo-housed mandrills *Mandrillus sphinx*. These authors studied the behaviour of a small group of mandrills occupying a traditional tiled-and-barred indoor cage at Zoo Atlanta and compared this with the behaviour of the same group after it had been moved to a large naturalistic outdoor enclosure. The behaviour of the animals changed in the new enclosure: time spent feeding, in locomotion, and out of sight increased, whereas time spent stationary, exploring, playing, and other social interaction decreased (**Table 4.4**). The hope, of course, was that these changes made the mandrills more similar to those in the wild. Unfortunately, no comparable data were available for wild mandrills, but the authors were able to compare their animals with two published studies of mandrills living in captivity, but in their native country in an enclosed area of natural forest. In one of these latter studies, the animals had ***ad libitum*** provisioning; in the other, they had limited provisioning. The zoo mandrills, after release into the naturalistic enclosure, were more like the mandrills with restricted

Environment	Time spent in behaviour (%)			
	Feeding	Moving	Stationary	Social
Zoo-housed (*ex situ*)				
Traditional/indoor	36	6	30	10
Enriched traditional/indoor	52	–	–	20
Naturalistic	66	7	12	6
Confined but in their range country				
Limited provisioning	64	–	–	–
Ad libitum provisioning	28	19	48	5
Unconfined in their range country				
Ad libitum provisioning (study 1)	22	20	45	13
Ad libitum provisioning (study 2)	29	25	39	–
No provisioning (study 1)	63	18	10	9
No provisioning (study 2)	47	21	22	10

Table 4.4 A comparison of some mandrill *Mandrillus sphinx* behaviours in different conditions across the wild–captive continuum*

*Data from Chang *et al.* 1999.

Note: The data for unconfined animals are for a different species, as data were unavailable for wild mandrills.

provisioning, but in their native forest. This is probably a good result, but it leads us to ask in what way the forest-enclosed animals differ (if at all) from unrestricted wild animals.

It was pointed out many years ago by Bernstein (1967) that, in order to be considered 'natural habitat', a field site should have space for all the life history requirements of the animals, little human disturbance, and little human effect on the habitat. Just how many of the field sites that have become well known as places in which to study wild animals actually satisfy these requirements is unclear. Hosey (2005) has attempted to define the characteristics that distinguish zoo environments from the other sorts of environment in which animals live, including the various sorts of 'wild'. He points out that zoo environments can largely be characterized by the extent to which they confront animals with human presence, require animals to live in what is sometimes a restricted space, and involve management of the animals' life histories. But these three characteristics are not unique to zoo environments; they are found, to a greater or lesser extent, in many 'wild' environments as well. Clearly, again, caution is needed in our interpretations of wild–captive comparisons.

Summary

- Behaviour is of interest because, among other things, it can tell us how an animal is being affected by the zoo environment and can give us clues about the animal's welfare.
- The behaviour that we observe is moulded by the animal's genetic make-up, but also by its experiences, and this makes behaviour very flexible.
- Zoos have advantages for collecting descriptive information about the behaviours that animals show, which would usually be much more difficult to observe in the wild.
- Aspects of the zoo environment may lead to changes in animals' behaviours. Both physical (cage size and complexity, food, zoo routine) and social (conspecifics and other species) aspects of the zoo environment may do this, but our knowledge of this, particularly for animals other than primates, is very incomplete.
- If zoo environments are poor, abnormal behaviours may result. Interpreting these is not easy, but, thankfully, they are much less of a problem for modern zoos, because modern housing and husbandry provide much better environments than were previously available.
- A possible benchmark for interpreting the behaviours that we see in the zoo is how the animal behaves in the wild, but we should be cautious about applying this too simplistically.

Questions and topics for further discussion

1. What can studying animals in zoos tell us about animal behaviour?
2. What evidence is there that the behaviour of zoo animals is changed by their captive environment?
3. Is the term 'abnormal' an appropriate description to use for stereotypies?
4. Is there any value in comparing the behaviour of animals in zoos with that of their wild conspecifics?
5. Do animals adapt their behaviour to the zoo environment?
6. If the behaviours that we see in zoo animals are no different from what we see in the wild, can we assume that captivity has no impact on the animals?

Further reading

There are many good textbooks available on animal behaviour, but several are restricted to functional interpretations of behaviour. Good coverage of all areas of the discipline is given by McFarland's *Animal Behaviour: Psychobiology, Ethology and Evolution* (1999), Alcock's *Animal Behavior: An Evolutionary Approach* (2009), and Manning and Dawkins' *An Introduction to Animal Behaviour* (2012). There are also many good texts on animal learning: a good starting place is Pearce's *Animal Learning and Cognition* (2008). Behavioural ecology is well explained in *An Introduction to Behavioural Ecology* by Krebs *et al.* (2012). A number of chapters in *Wild Mammals in Captivity* (Kleiman *et al.* 2010) deal in more depth with some of the areas covered in this chapter. An introduction to methods of undertaking behavioural research can be found in Martin and Bateson's *Measuring Behaviour: An Introductory Guide* (2007) and Dawkins' *Observing Animal Behaviour* (2007).

For specific information on carrying out behavioural research on zoo animals, the best sources are the BIAZA research guidelines, which are available online at **http://www.biaza.org.uk**. Currently, available guidelines include those on project planning and behavioural observations (Wehnelt *et al.* 2003), visitor studies (Mitchell and Hosey 2005), surveys and questionnaires (Plowman *et al.* 2006), statistics for zoo research (Plowman 2006), and personality profiling (Pankhurst *et al.* 2009).

See also **Chapter 14** on 'Research'.

Websites and other resources

For anybody who wants to know more about animal behaviour, the websites of the Association for the Study of Animal Behaviour (ASAB) (**http://asab.nottingham.ac.uk**) and the Animal Behavior Society (ABS) (**http://www.animalbehaviorsociety.org**) provide a great deal of information and also links to other behaviour-related websites.

The International Society for Applied Ethology (ISAE) caters for those who are interested in applied aspects of animal behaviour, such as the effects of captivity and human interaction. Its website (**http://www.applied-ethology.org**) contains relevant information and links.

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.
http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Chapter 5
Animal identification and record-keeping

Being able to identify individual animals in a zoo is essential for monitoring their health, promoting good welfare, cooperating with conservation initiatives, and undertaking research. In this chapter, we will provide an overview of the diverse methods used to identify individual captive animals, and will also discuss the relative merits and drawbacks associated with some of them. When animals can be individually identified, the amount of information that can be recorded about them is almost limitless, which means that keeping comprehensive animal records is also an important part of captive animal management. It probably sounds a little dull and uninspiring, but record keeping is the cornerstone of good captive animal management and informs all the decisions that we make about animals in zoos. So in this chapter we will explore the need for keeping standardized records that are easily accessible, and the systems that are in place to make this possible. These range from record cards, to a computer-based program called the Animal Records Keeping System (ARKS), and its sister programs, and on to the Internet-based Zoological Information Management System (ZIMS), which is now a reality and which promises to revolutionize the way in which zoos manage their animals.

The topics that we will cover in this chapter are as follows.

5.1   **The importance of knowing your animals**
5.2   **What species? Nomenclature and taxonomy**
5.3   **Identifying individual animals**
5.4   **Temporary artificial methods of individual identification**
5.5   **Permanent artificial methods of individual identification**
5.6   **Record keeping: what information could, or should, be recorded?**
5.7   **Zoo record keeping systems**

In addition, there are several boxes exploring related issues about **scientific names** and the use of molecular techniques, as well as an explanation of the standard units used to measure different kinds of animal.

5.1 The importance of knowing your animals

Successful animal management is dependent on knowing your animals: knowing what they had for breakfast, what has happened to them in their lives, their medical history, how related they are to other animals in their group or the captive population, and so much more. If you know these things, then you can make decisions about their daily management and care, and also plan their long-term management within the captive population,

Common name	Scientific name	Group at 1 January 2007	Arrive	Born	Death within 30 days of birth	Death	Depart	Group at 31 December 2007
White-naped crane	*Grus vipio*	2.1.1	0.2.1	0.0.2	0.0.1	1.0.0	0.1.0	1.2.3

Table 5.1 An example of the information that should be provided in zoo annual reports, using the white-naped crane *Grus vipio* as an example*

*It is customary within zoo records to summarize group compositions as the number of 'males.females.animals of unknown sex', e.g. '2.1.1' refers to two males, one female, and one unknown.

such as their potential breeding prospects. If you do not know, or cannot recognize, your animals at an individual level, it becomes very difficult to monitor them and you are then likely to miss any changes in them that might reflect their health or welfare status. Being able to identify individual animals is also essential when assigning parentage to offspring, which is a fundamental requirement when managing small populations, especially when making recommendations about who should or should not breed (see **Chapter 9** for an overview of small population management). Because of this, it is a legal requirement for all UK zoos to keep records for individually recognizable animals, or groups if the individuals cannot be identified (Defra 2012a; see **section 5.6** for more on this), and to produce an annual report that details some of this information (see **Table 5.1**).

As we can imagine, however, while recognition and record keeping is reasonably straightforward for a small number of animals, it becomes more difficult as the size of the group or collection gets bigger. For example, on 30 June 2012 the living collection in Zoos Victoria (encompassing the sites Melbourne Zoo, Werribee Open Range Zoo, and Healesville Sanctuary, Australia) numbered over 3,536 individual animals, representing over 330 species (Zoos Victoria 2012). This is a lot of animals for which to keep records. Fortunately, there are many processes in place to facilitate the identification of individuals and the keeping of detailed records about them.

There are two main reasons for keeping records for individual animals: to ensure good health and welfare, and to aid conservation via support for **captive management programmes**. Let us look more closely at each of these.

5.1.1 Animal records for health and welfare

The health and welfare of individuals can be more easily monitored if the animals can be recognized individually. Therefore it follows that the health and welfare of individually recognizable animals is likely to be greater than that of animals in groups, within which an animal might have to show exaggerated signs of ill health or poor welfare to be noticed among the crowd. By comparing the records of many animals, it is also possible to establish what is 'normal', and thus discern whether any changes that can be seen are usual for an animal of that age, sex, and species (see **section 5.6.6**).

Record keeping is also important during the transport of live animals, because transport potentially increases the risk of disease transmission and has been found to be stressful for many species (see **section 6.3.2**). There is much legislation and regulation with regard to health, welfare, and conservation governing the live transfer of wildlife (Cooper and Rosser 2002; see also **Chapter 3**). When good records exist for individual animals, it is possible to track the movements of animals, and this enables the authorities (within the UK, the Department for Environment, Food and Rural

Affairs (Defra)) to map any disease spread and to prohibit any animal transfers that may increase disease transmission. Thus, the risk of transferring disease can be reduced, because movements of animals can be restricted to ensure that healthy and unhealthy animals are kept separate. This has been demonstrated in domesticated animals, where individual identification and the presence of good records greatly enhance disease prevention and control (Disney *et al*. 2001).

5.1.2 Animal records for conservation

Using records to restrict the transport of live animals is also necessary to safeguard wild populations. As previously mentioned, animals that are listed under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (UN 1973) as endangered or threatened (see **section 3.2.1**) cannot be transferred without appropriate permits and licensing, to reduce the likelihood that endangered animals are being traded commercially, which would put pressure on declining wild populations.

Keeping records of animals' rearing and movements is also necessary to facilitate captive management programmes. Nowadays, animals rarely enter captive management programmes from the wild, but, if they do, they need to be classified into the appropriate species or subspecies category (more about this in **section 5.2**). For those born in captivity, simply being able to recognize dams and sires of new offspring will greatly increase the accuracy of any genetic and **demographic** analyses (carried out using records) performed to inform recommendations for that captive population.

Comparing information collated between many zoos enables **epidemiological** research to be undertaken and this can identify trends within the captive population, such as the incidence or spread of disease, as well as **fecundity** and/or **mortality** rates. Such studies have included the investigation of fecundity and mortality in zoo elephant populations (Clubb *et al*. 2008; Clubb *et al*. 2009) and mortality in zoo cuttlefish *Sepia officinalis* and parrot populations (Sherrill *et al*. 2000; Young

et al. 2012). Results of such studies positively feed back into the management of the animals, and this facilitates improvements in health, welfare, and conservation of the captive population.

5.2 What species? Nomenclature and taxonomy

One of the first things that should be identified about an animal in a zoo is what sort of animal it is. To ensure that an animal is kept in an appropriate social and physical environment, and that it is fed on the most appropriate foods, we need to know to what species it belongs. Indeed, for managing its contributions to the captive breeding and conservation of its species, we often need to be more precise than this and determine to which subspecies it belongs. Vernacular names of animals are very variable and tell us little about the animal except that we think we know what it is. For example, the names 'red fox' and 'grey fox' may tell someone that we are referring to something that is small and dog-like, but if we were to say 'flying lemur', we would be talking about an animal that, in fact, is not a lemur (and does not fly either). In Germany, the red fox is *Rotfuchs*, and in France it is *renard*, and given that this animal lives throughout Europe, Asia, and North America, there are doubtless dozens of other names for it as well.

To ensure that we all know precisely what animal we are talking about, we use a system of scientific nomenclature, whereby each species is given a unique **binomial name** in a Latinized form (Latin is no longer widely used as a first language, so it is ideal for this, although some scientific names are derived from Greek, rather than Latin, words); these names are then organized within a system of classification or **taxonomy**, which tells us much more about the animal than merely what it is. For example, taxonomy can give us information about the distinctiveness and variability of the species, and can also help us to understand its evolutionary relatedness to other species.

It is worth looking a little more closely at these systems.

5.2.1 Binomial nomenclature

The basis of the scientific naming system for animals (and for plants as well) is that each species has a name made up of two components (which is why it is called 'binomial'), one which identifies its genus (its generic name) and one which identifies its species (its specific name). The words used for the generic and specific names can come from any language, but are written in a Latinized form. Thus, the red fox referred to above has the binomial *Vulpes vulpes* (from the Latin *vulpinus*, a fox), and the grey fox is *Urocyon cinereoargenteus* ('silvery-grey with a dog's tail', but a mixture of Greek and Latin). Note that generic names start with a capital, but specific names start with lower case. The scientific name[1] of an animal is always italicized (or underlined if handwritten).

This system was devised by Carl Linnaeus[2] (1707–1778) (**Fig. 5.1**), initially for naming plants, but later extended to animals. The starting point for modern animal nomenclature is the tenth edition of Linnaeus' *Systema Naturae*,

Figure 5.1 Carl Linnaeus (1707–1778), who devised the binomial system of animal (and plant) taxonomy, seen in this 1737 painting in Lapp costume. (Photograph: Biodiversity Heritage Library/Missouri Botanical Garden/CC-BY)

which was published in 1758; any Latinized names that date from before this are not considered to be valid.

The process of applying this system is subject to strict rules, overseen by the International Commission on Zoological Nomenclature (ICZN); one important rule is that of priority, whereby the first valid name for a genus or species is the one that must be used. What makes a name valid is subject to informed debate, but decisions on this can lead to animals being renamed (see **Box 5.1**). All of this may seem very pedantic, but it is essential if we are to have confidence that the names we use are systematic, comprehensive, unambiguous, and understood throughout the world.

As an example of how this works, let us return to our fox example. Linnaeus considered the fox to be a kind of dog and gave it the binomial *Canis vulpes*. But later scientists considered that the fox was sufficiently different from domestic dogs and wolves to be distinguished by a different generic name, *Vulpes*. The North American red fox was thought by the zoologist Desmarest to be a different species, which he named *Vulpes fulva*. Nowadays we regard these two as the same species, but since the name *fulva* dates from 1820, Linnaeus's name *vulpes* has priority, and is how we know the species.

When Linnaeus devised his binomial system, species were seen as fixed entities that would not change. We now know that species change over time through evolutionary processes. One consequence of this is that different populations of the same species living in different areas can become different from each other in their morphology and behaviour. These populations may be regarded as subspecies, and given a third Latinized name (a trinomial) to distinguish them from the other subspecies. In this case, the population on which the original species description is based is given a trinomial that is the same as the

---

[1] It is more correct to talk about the 'scientific name' of an animal than the 'Latin name', because some of these names are derived not from Latin, but from classical Greek (or even a hybrid of the two, like the grey fox).

[2] For many years, Linnaeus was a professor at the University of Uppsala in Sweden, and his house and garden in Uppsala can still be visited.

Box 5.1 THE NAMING OF ANIMALS: WHO IS RIGHT?

We have stated in **section 5.2.1** that the scientific binomials that we use to identify animal species can sometimes change because of taxonomic rules such as the rule of priority. So how can this happen?

An animal's specific name is most likely to change if it is discovered that what we thought were two different species are only one, or if what were thought to be separate subspecies of the same species are judged to warrant being regarded as distinct species in their own right. Generic names can change if new evidence suggests that a genus is not really distinctive enough to warrant its own name or, conversely, that the known members of a genus are sufficiently diverse that they really ought to be regarded as belonging to more than one genus. But we have also said that decisions such as these are matters of informed judgement. So, whose decisions are right?

The answer really is that nobody is right, but rather that a consensus of support develops for particular viewpoints. In one sense, giving a species a binomial name is akin to formulating a hypothesis about its evolutionary relationships, so

we make our decisions on the basis of how much the evidence supports that hypothesis. But in that case, which names should we use? Fortunately, consensus views are usually available for people to refer to; these are often called taxonomic authorities and allow us to check that we are using the currently accepted name for a species. We have tried to be consistent and to use accepted taxonomic authorities for the animal names to which we refer in this book. For mammals, the most widely used authority is Wilson and Reeder (2005). This is an enormous book (over 1,300 pages), but, fortunately, it forms the basis of the Mammal Species of the World (MSW) database hosted by the Smithsonian Institution (currently at **http://nmnhgoph.si.edu/msw/**). The equivalent authority for birds is Sibley and Monroe (1990, 1993), which is also available as a database on the Internet (currently at **http://www.ornitaxa.com/SM/SMOrg/sm.html**). Similar Internet databases exist for amphibians (hosted by the American Museum of Natural History at **http://research.amnh.org/herpetology/amphibia/index.php**) and reptiles (at **http://www.reptile-database.org/**).

specific name. To return to our foxes, Linnaeus's original description was based on the Scandinavian fox, so that is now referred to as *Vulpes vulpes vulpes*, whereas other foxes have different trinomials (for example, *Vulpes vulpes fulva* for the American red fox).

5.2.2 Taxonomy

At this point, we might ask: what do we actually mean by 'genus' and 'species'? Whole books have been devoted to answering this question and there is no unequivocal answer. A commonly used definition of the species is the biological

species concept[3] of Ernst Mayr (1942), which states that '*species are groups of interbreeding natural populations that are reproductively isolated from other such groups*'. This reproductive isolation may be the result of living in different areas (allopatry), having different morphologies (for example, reproductive organs that do not fit with each other) or different behaviours (for example, courtship patterns that are not recognized by each other), or the consequence of post-copulatory mechanisms (for example, different **chromosome** shape or number leading to failure of meiosis (see **section 9.1.1**) and hence rendering offspring infertile).

[3] The biological species concept is that species are populations that are reproductively isolated from, and hence unable to breed with, other populations (Mayr 1942). This is usually difficult to apply, so morphological or genetic criteria are often used instead.
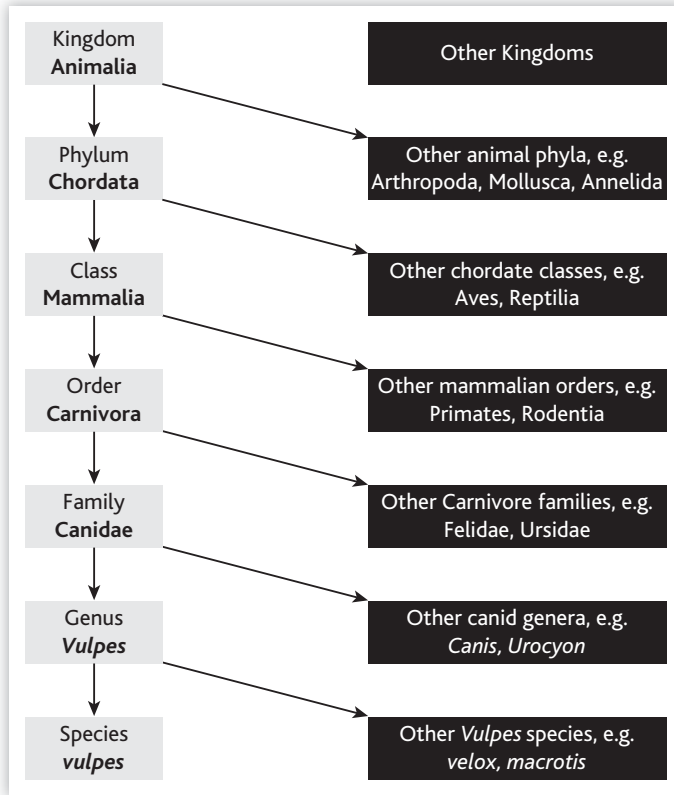
Figure 5.2 The classification of animals is based on a hierarchical system, within which each grade (e.g. class, order, family) encompasses examples of the next lower grade. Here, you can trace the classification of the red fox through these grades and also how the fox is related to other species.

This is still a useful definition, not least because it is, in principle, testable—but it is not easy to test and is not of much use to palaeontologists. In practice, judgements based on differences in morphology, reproductive isolation, and how different populations are at the molecular level are used to decide whether similar, but different, populations represent different species or just subspecies of the same species. Similar judgements are used to decide if similar species all belong to the same genus, or whether they are different enough to warrant different genera. In our fox example, European and American red foxes are reproductively isolated by virtue of living on separate continents, but European foxes that have been introduced into North America breed readily with the native foxes. However, two other North American species, the kit fox *Vulpes macrotis* and the swift fox *Vulpes velox* (**Fig 5.3**), do hybridize with each other and thus may actually be just one species. But our grey fox, also a North American species, is sufficiently different from these three

to be placed in a different genus, *Urocyon*. Genera are best regarded as monophyletic[4] assemblages of related species.

Both genus and species are grades within a taxonomic system that shows how all species are related to all other species. The main grades in this system are as follows and the system is hierarchical, which means that each grade is ranked higher than the next grade: kingdom; phylum; class; order; family; genus; species. We can use our fox example again to see how this works (**Fig. 5.2**).

The way in which we classify animals reflects their evolutionary history, as we have seen in the discussion about what constitutes a genus. Because of this, taxonomy tells us more than only the name of a species; it also tells us who its relatives are (which other species are in the same genus), how variable it is (how many subspecies there are), and how unusual it is (how many others are in the same group).

[4] Monophyletic means having one recent common ancestor.

Figure 5.3 Swift foxes *Vulpes velox* are critically endangered. This dam is tracked using a radio-collar so that her reproductive success can be monitored. (Photograph: Sam Bremner-Harrison).

5.2.3 Relevance to zoos

Although our taxonomic system is intended to reflect what we think is the evolutionary ancestry of different animals, we need to bear in mind, firstly, that it is nevertheless an artificial system. Phyla, classes, and orders have no reality outside our classification system, and they represent our attempts to put order on to our knowledge of the natural world. Secondly, decisions about which animals belong in which taxonomic group are matters of informed judgement, and therefore can change as knowledge and techniques improve.

It is decisions about the species and subspecies grades that are most likely to affect zoos, because these can have consequences for the way in which social groups are set up and breeding is managed. There is, for example, an issue about whether species or subspecies should be the grade at which conservation imperatives are decided (see **Chapter 10**). For this reason, zoos nowadays need to know not just which species, but which subspecies, they have. And, of course, to do this they need to have access to the most up-to-date taxonomies (see **Box 5.1**).

5.3 Identifying individual animals

There are many ways of distinguishing individual animals, but these methods vary in their reliability, how much they need trained staff, their costs,

and how much impact they have on the animal itself. Some methods have benefited from a fruitful exchange of ideas between field workers and zoo professionals. Many field workers may not even be able to see their animals, so they are very reliant on indirect animal identification methods, such as using faecal samples or nests, which may allow the identification of species or, possibly, individuals (e.g. Bowkett *et al.* 2009). In contrast, finding animals in a zoo should not be such a problem and thus it is usually possible to use direct animal identification methods, such as using visible characteristics.

There are a number of ways to achieve individual animal identification, but whatever method is used, it should aim to meet a set of basic standards.

1. Pain, suffering, or any change in the animal's behaviour as a direct, or indirect, result of the identification method chosen should be minimal.
2. Identification of the animal should be possible from a distance, to avoid the need to handle it.
3. The method used should ideally be long-lasting, again to avoid recurrent handling.
4. The method used should be acceptable to the zoo's visitors (see **section 6.1.3** for a discussion of the need to integrate the needs of visitors into animal housing and husbandry).

A variety of animal identification methods are summarized in **Table 5.2**. Some of the advantages and disadvantages associated with these different methods are discussed in more detail in the next two sections.

5.3.1 Using naturally occurring characteristics

When you look at animals, it is often possible to notice natural markings or characteristics that appear to distinguish one animal from another, and these can provide a useful tool for individual animal identification. Naturally occurring differences between individuals include: colour or

Method	Description/ location	Temporary (T) or permanent (P)	Comments	Examples
Natural markings	For example: coat colour or pattern; physical deformity; size	P**	Cheap and easy. Requires skilled staff and obvious differences between animals	Okapi: stripes (**Fig. 5.5**) Tiger: spots
Branding	Flanks; horns	P	Painful	Snakes: freeze branded (**Fig. 5.16**)
Tattoo	Skin around eyes, rump, or on fingers	P**	Painful	Macaques: ischial callosities
ID cuts	Ears; horns; digits	P**	Potentially painful	Wildebeest: horn notches Rhino: ear holes Lizard: digit removal
Microchips, transponders	Injected under the skin	T	Painful and may require sedation Potential migration under the skin	Everything, from dormice to elephants (**Fig. 5.14**)
Adornments	Tags such as ear tags; beads threaded through skin	T	Potentially painful. Usually attached to young animals	Blue iguana: beads (**Fig. 5.13**) Mara: ear tags (**Fig. 5.12**)
	Rings or collars worn by animal	T	Potential risk of entanglement	Ringtailed lemur: necklaces (**Fig. 5.7**) Bird: leg rings (**Fig. 5.10**) Penguin: flipper rings (**Fig. 5.11**)
Clipping	Hair; feathers	T	May be difficult to see from a distance; hair will re-grow	Rarely used in zoos
Dye/markers	Ram pads; spray; paint; stuck-on markers	T	May transfer onto other animals Need to ensure non-toxic material used	Beetles: paper numbers (**Fig. 10.6**) Tortoises: painted dots

Table 5.2 An overview of some methods used to identify zoo animals individually*

*Listed in order of permanence, with more permanent methods first. Considerations are provided that need to be balanced against the need to identify individuals.

**Characteristics may change over time, due to ageing or other factors such as pregnancy, new feather growth, injury, etc. This is especially true for colourful or shaped identifiable features.

patterns in coat, feathers, or skin; facial and bodily characteristics and features, including deformities (such as a twisted leg or scars, with which the animal may have been born or which may have occurred during its lifetime); size; behaviour.

Visible characteristics are an obvious and practical method of identifying individuals on a daily basis, but this technique is reliant on the observer's skills at consistently recognizing differences between individuals, or identifying the features that characterize a certain individual. Many keepers are able to recognize the animals in their care this way, without the need to use artificial identification methods, but their ability to do this is dependent on their experience and familiarity with the animals, and also on other factors relating to the animals and their housing. As group sizes get bigger, it becomes more difficult to recognize animals individually, because the number of identifying features required also increases and recognizing these can become increasingly complicated. Similarly, enclosure type can affect individual recognition, because enclosures that enable animals to distance themselves from keepers can make the identifying marks more difficult to see (although binoculars can obviously help in this instance).

Visual characteristics are prominent in a lot of different species, but when you look at these (for example, **Fig. 5.4**) it is clear that they do not

necessarily make individuals easy to identify. Obviously, the degree to which characteristics vary between individuals will influence how easily they can be recognized. Trying to recognize individual zebra from their stripes, for example, can seem difficult if you look at a herd of zebra within which the individual animals are in close proximity to one another. If you concentrate on only one area of the zebra, however, and compare the pattern you see with that of the same area in other zebra, the task becomes a bit more manageable (**Fig. 5.5a**). This can work with other species as well: for example, okapi *Okapia johnstoni* (**Fig. 5.5b**).

Indeed, sometimes, a relative measure of visual appearance is used, where a process of elimination allows the identification of individuals; for example, 'Fred is the largest in the group'. One problem with doing this is that it requires more than one animal to be in your field of vision at the same time, and it also usually needs those animals to be in close proximity to one another, so that comparisons of size, colour, or some other characteristic can be made. Because of this, there are clear advantages in being able to recognize the identifying feature in each individual independently of what the other animals in the enclosure look like.

On a more practical note, we should remember some limitations on the usefulness of natural characteristics. Firstly, the visibility of some

Figure 5.4 A huge array of colours and patterns are present in the animal kingdom, but these do not necessarily help us to distinguish between individuals. For example, look at these zebra. How well can you distinguish individuals here? (Photographs: Vicky Melfi)
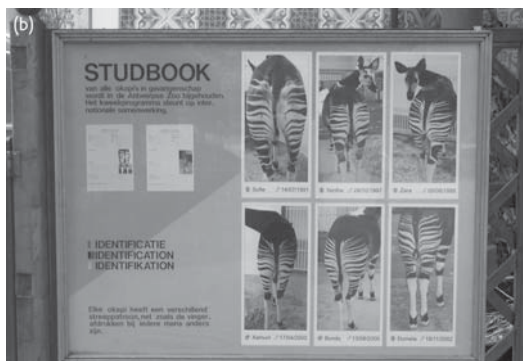
Figure 5.5 If you concentrate on one area of the animal, sometimes it can become easier to distinguish individuals. For example, if you look at the rear patterns of (a) these zebra or (b) these okapi *Okapia johnstoni*, it becomes easier to recognize differences between individuals. (Photographs: (a) Paignton Zoo Environmental Park; (b) Vicky Melfi)

characteristics may be affected by the animal's behaviour; for example, broken digits may only be visible when animals are holding objects or using their hands, or a distinguishing mark or feature may be hidden when an animal sits or lies down. Secondly, some natural markings and characteristics may change over time. For example, as animals get older, their coats may change colour, particularly by losing colour or becoming grey or patchy, and their postures and behaviours may also change. Similarly, the weights, and thus sizes, of animals are also likely to vary over time

because of changes in age, diet, social position, and reproductive status.

It is likely that the individual identification of a large number of animals from their natural characteristics can only really be accomplished by a small group of people who are most familiar with them, such as their keepers. But, in many situations, a larger body of people, such as other keepers, the vet, and researchers, will also need to be able to identify individual animals, and these people will not necessarily have either the time or the expertise to be able to use natural visual characteristics. In these situations, or when direct observation of differences between animals is not sufficiently reliable because of limitations such as those outlined above, using artificial methods to identify animals individually is probably a more satisfactory method.

5.3.2 Using artificial methods of individual identification

A wide variety of artificial methods can be used to identify animals individually, ranging from leg rings[5] and necklaces, to tattooing and transponders.[6] The choice of method is usually more informed by keeper experience and tradition than by scientific assessment of the impact or efficacy of the method, mainly because so few studies have been carried out in this area and therefore our knowledge is limited. It is also important that the ethical and welfare implications of using the different methods is considered. If the method used allows the animal to be identified and the keepers feel that its behaviour is unaffected, the method is considered successful and its use may subsequently spread elsewhere by means of positive anecdote.

In determining which artificial identification method should be adopted, several interrelated factors should be considered. Is temporary or

---

[5] Rings used for animal identification are often referred to as 'bands' in the USA.

[6] It should be noted that the term 'transponders' may refer to devices with or without a battery supply which, respectively, are able to broadcast information or require a device to read the information directly. Within the zoo industry, 'transponders' and 'microchips' refer to the latter devices—that is, those that do not have their own battery supply.

permanent identification required? What degree of intervention, invasiveness, or pain is acceptable? What information needs to be portrayed and should it be visual? Which methods have been successful with the target species? What level of security (reliability) is acceptable?

Let us look more closely at each of these in turn.

Temporary versus permanent methods

One of the aims of animal identification is that it should be as long-lasting as possible, so we would expect that those methods that are more permanent would generally be favoured over temporary measures. However, there are some situations in which temporary methods are sufficient. For example, when newborn animals in large groups need to be identified, marking them with a spot of dye, or shaving or clipping fur or feathers in a known location to create a distinctive coat pattern, can allow them to be monitored. Similarly, animals that have been recently moved into a new group may be marked only until their keepers are able to recognize them using visual characteristics. Eggs being incubated, a temporary process, are often numbered with a pencil for identification. The lifestyles of some animals can help increase the longevity of temporary measures, if the animals do not interfere with the identifying marker. Examples of this include using paint on iguana skin and tortoise carapaces, or sticking a marker onto a beetle (**Fig. 10.6**).

Surprisingly few methods of individual identification can be viewed as permanent. Usually, permanent methods of identification are achieved by making physical alterations to the animal's body that will withstand time. These alterations may include identification cuts, **branding**, and tattooing, and therefore are sometimes referred to as 'mutilations' (see **section 5.5**). In contrast, temporary methods of identification are achieved either by making temporary physical changes to the animal's body, such as colouring or clipping hair, skin, or feathers, or by adding something to the animal's general appearance using **adornments** such as tags, rings, or necklaces (see **section 5.4**).

Transponders (sometimes known as 'microchips') are not visible, but can migrate within the animal's body and thus be lost and no longer read, or they can be groomed out by an attentive **conspecific**, and so cannot be considered permanent.

The longevity of temporary measures can vary significantly. With luck, some temporary measures of identification can last for an animal's lifetime, although it is likely that, over time, they will become indistinct or will be lost. There is a tendency to presume that adornments (temporary) should be chosen over mutilations (permanent), because the latter have negative connotations. But the relationship between the type of identification method used and the animal's welfare is not that straightforward, because the degree of intervention, invasiveness, and potential for pain is variable with both temporary and permanent types of identification.

The degree of intervention, invasiveness, and pain that results

When choosing between temporary or permanent methods of individual animal identification, it is necessary to consider and weigh up the following factors.

1. *The degree of handling necessary*   All methods of artificial individual identification require the animal to be caught up so that the 'identifying feature' can be applied. This can take time and effort, and may be stressful to the animal.

2. *The potential for pain that may be experienced when applying the identifying feature*   This can be highly variable, ranging from the slight discomfort resulting from the application of a leg ring (which is probably negligible compared with the stress of being caught up), to the certain pain that an animal experiences when its ear is pierced for an ear tag, its skin is scalded with extreme cold or heat during branding, or during the amputation of a digit, to the invasiveness of sedating an animal in order to implant a transponder subcutaneously. We will return to this issue when we consider different methods of identification later in this chapter.

3. *The longevity of the identifying feature* That is, how long it will be before the process needs to be implemented again. It should be remembered that all temporary measures of individual identification are just that—temporary. We have to bear in mind that, at some stage, the process has to start all over again and another 'identifying' feature has to be applied to the animal depending on the longevity of the method chosen. With methods such as colouring or clipping the fur, feathers, or hair, the longevity of the identifying feature may be quite short. Thus, methods that are longer lasting are favoured, because the need to catch and restrain the animal can then be minimized.

4. *The impact that the identifier may have on the life of the animal* This is probably the least easy question to answer, so we will now look at this last consideration in a bit more detail.

Whether the marker or identifier will affect the animal behaviourally or physically during its everyday life has not been fully explored. Most studies of this kind have been conducted on laboratory-housed animals or those living in the wild, and sometimes the effects can be quite unexpected. For example, laboratory-housed zebra finches *Taeniopygia guttata* became attracted to the differently coloured leg rings of other finches, with females having a preference for red rings on males and males preferring black rings on females (Burley 1985). Interestingly, these colour preferences seemed apparent only in laboratory conditions, within which ultraviolet (UV) light is available; we know that UV light plays a fundamental role in bird perception (Hunt *et al.* 1997). Other studies of wild birds found that some methods of individual identification put demands on the birds that hindered their survival, by increasing mortality or reducing reproduction (reviewed by Gauthier-Clerc and Le Maho 2001; Jackson and Wilson 2002). For example, Culik *et al.* (1993) demonstrated that Adelie penguins *Pygoscelis adeliae* with flipper rings used significantly more energy (24 per cent more) when swimming compared with those without rings.

It certainly appears that some methods of artificial individual identification are associated with problems, while others are not. Leg rings are sometimes reported to be deleterious, but may also be reported as better than alternative methods (such as wing tagging[7]), or may even be viewed as having no consequence at all for the animal (Kinkel 1989; Cresswell *et al.* 2007).

Similarly, some individual identification methods appear to impact on mammals, while others do not. For example, ear transmitters (transponders powered with batteries, so that they broadcast information) used in moose *Alces alces* calves were thought to be associated with a decreased likelihood of survival, whereas, in fact, the survival of calves with ear tags was no different from that of calves without any form of individual identification (Swenson *et al.* 1999). Nevertheless, studies on laboratory-housed and wild animals do demonstrate that individual identification methods may have an impact on their lives, so it is something that needs to be considered.

However, it is likely that captive conditions may mitigate some of these problems, because plentiful food, veterinary treatment, and the removal of many of the other pressures that the animals would have in the wild ensures their survival in captivity. Because of this, zoo populations may be ideal for trying out new individual identification methods or modifications to existing ones, so that they can then be tailored to have as little impact as possible on wild animals. Zoo animals, in turn, gain from these advances in knowledge and technology. An example of this is the study by Simeone *et al.* (2002), who trialled data loggers on zoo-housed Humboldt penguins *Spheniscus humboldti* before using them in the wild.

We started this section by identifying four different aspects on which to judge individual identification methods. Each identification method may rate differently on each of these scales, so the net effect of each method should be considered.

---

[7] Wing tagging refers to the addition of a tag to a bird's wing. Tagging can more generally refer to applying a tag, such as an ear tag, to any animal.

For example, feather clipping is not painful, but the quick regrowth of feathers will require frequent catch-ups of the birds—a procedure that can itself be stressful to the animal. Alternatively, applying a tattoo is painful (although this might be mitigated to some extent with **analgesic drugs**) but, once applied, it should provide a clear individually identifiable feature for the rest of the animal's life. We should also take account of the species and individual differences between animals, and the housing and husbandry regime in place, when deciding which method is most appropriate. For tame or trained animals, catch-ups may not be stressful, so repeating or replacing 'non-painful' methods may be considered best. However, for animals that are very wild and become stressed during interactions with keepers, the use of a permanent method of identification that only needs one handling session is ideal.

Portraying information

In most situations, identification methods aim to convey the pertinent information about an individual animal that is necessary for its day-to-day management. Artificial methods of identification can provide that information quickly and effectively to anyone who knows how to interpret it (see following section on 'Codes'), unlike natural markings, which usually rely on the keepers' skill and knowledge of individual animals. For animal management, the best identifying features are those that can be seen clearly without the need to catch or restrain the animal. Currently, this cannot be achieved with subcutaneous microchips and transponders, even though they are widely used, although technological advances may soon change this (see **section 5.4.3**). Many zoos use more than one method to identify their animals individually, usually using transponders in conjunction with a visible feature, either natural markings or artificial markers.

At this stage, it is necessary to mention the perceptions of zoo visitors. Are their expectations of seeing wild animals in a **naturalistic enclosure** compromised by the sight of bright orange ear tags or other high-visibility identifying features?

This has not been empirically studied, and despite findings suggesting that the visitors do not necessarily perceive 'non-natural'-looking enrichment in naturalistic enclosures negatively (McPhee *et al*. 1998), there is still a tendency for zoos to adopt one of two approaches. Firstly, zoos can use identifying features that are less visibly obvious. These are only effective in animals that are comfortable with coming close to their keepers and are obviously useless if the animal is some distance from their keeper. For example, **notching** underneath a **chelonian** carapace can be used to identify individual animals, but requires the keeper to feel along the carapace, so he/she must clearly be very close to the animal.

Secondly, zoos can incorporate the identifying features into the education and interpretation provided to the visitor. An example of this is to give visitors the information that enables them to identify animals for themselves using natural markings, and this can be done by providing photographs of individuals (**Fig. 5.6**) or by highlighting their different patterns. Another way is to draw the visitors' attention to the artificial identifying features that the zoo uses to recognize its animals. For example, individuals in a large troop of ringtailed lemurs *Lemur catta* at Edinburgh Zoo were fitted with differently coloured pendants hung from necklaces. A corresponding poster next to the enclosure illustrated to visitors how to use these tags to identify individual lemurs and how they were related to each other (**Fig. 5.7**).

Codes

The information conveyed by the identifying feature is often coded. The simplest way of doing this is to allocate a number or letter code to an individual animal and transfer it directly onto the animal's body, or indirectly via an adornment. Whether putting information directly or indirectly on animals, the space available for this should be kept to a minimum, rather than writing the animal's name or number down the whole side of its body.

This has led to the creation of a number of different coding systems that can portray more information with less space. Often, combinations

(a) JOSEPHINE { The Momma }
Female
Sumatran Orangutan
Born: Circa 1960
Wild born
Arrived in San Diego: February 1, 1993
Weight: 125 lbs.

(b) Satu { The Class Clown }
Male
Sumatran Orangutan
March 26, 1995
San Diego Zoo
72 lbs.

(c) Indah { The Rebel }
Female
Sumatran Orangutan
Born: July 23, 1986
Adelaide Zoo, Australia
Arrived in San Diego: 1992
Weight: 115 lbs.
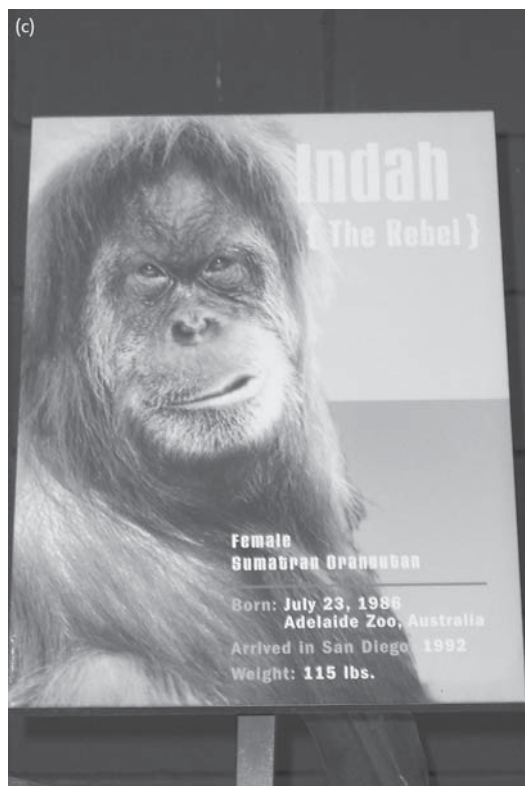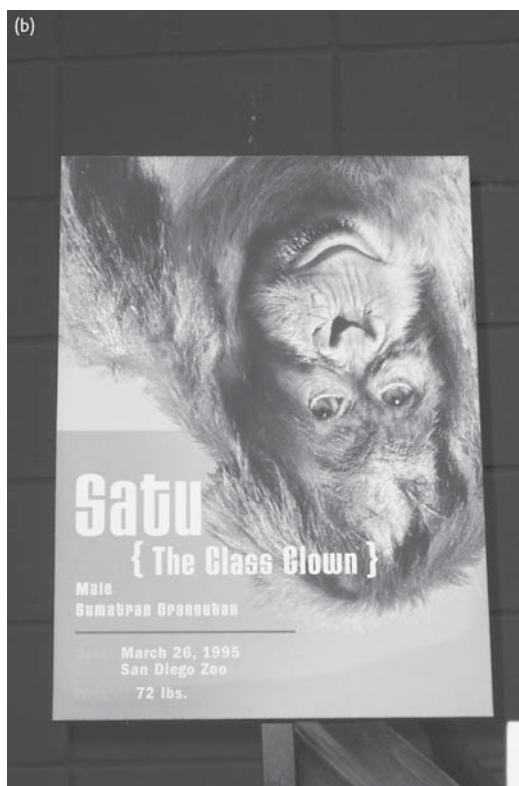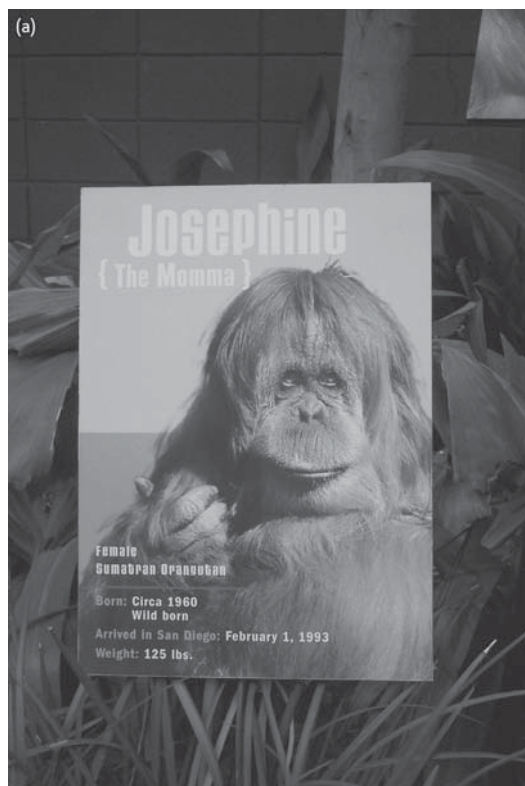
Figure 5.6 Illustrating the natural differences of animals to zoo visitors can be achieved by providing them with photographs of the animals. San Diego Zoo provides these pictures of their orang-utans *Pongo* spp. for visitors to be able to identify the animal at which they are looking (a, b, and c are different individuals). (Photographs: Vicky Melfi)

Figure 5.7 To the untrained eye, ringtailed lemurs *Lemur catta* all look very similar. But you can recognize animals individually if they have an identifying feature. In this example, lemurs at Edinburgh Zoo wear necklaces with different-coloured pendants. (Photograph: Julian Chapman)

positioning of an ear or wing tag, with tags on the left denoting males and tags on the right denoting females; as with all codes conventions can vary between zoos. These sorts of code have to be decided upon and adhered to at the different organizational levels in which they are used. At the level of an individual zoo, the position of the marker may be used to denote something like the sex of the animal; at a national level, there may be other marking requirements. In the UK, Defra requires all **bovids** to have ear tags with identity codes stamped on them. At a regional, or even global, level, other practices may be in force: the Conservation Breeding Specialist Group of the International Union for the Conservation of Nature (IUCN), for example, recommends using transponders that are ISO-compliant (CBSG 2004), and that implantation of the transponder must occur subcutaneously at standardized locations (Cooper and Rosser 2002) (see **Table 5.3**).

When physical changes are made to animals as a form of identification, numbering systems are frequently used in such a way that a large number of animals can be distinguished from each other by using permutations of a simple code. For example, tattooing spots around the eyes is one method of identification and, if the numbers 1, 2, 4, and 7 are represented around the left eye and values 10 20, 40, and 70 are represented around the right eye, different permutations of spot

of colours, numbers, and letters, in conjunction with their position on the animal's body, are used to convey the required information. For example, a zoo may denote an animal's sex through the

Taxa	Location
Fish	Base of dorsal fin or within the coelomic cavity
Amphibians	Lymphatic cavity; cover wound with tissue glue
Reptiles	
Snakes and lizards	Dorsal side of the tail base
Chelonians	Hind shoulder
Birds	Pectoral muscle or left thigh
Mammals	Behind the ear, at base or between shoulder blades, left of centre

Table 5.3 Globally recognized implantation sites for transponders*

*To increase the usefulness of transponders (so that they can be relocated and read), they should always be implanted on the animal's left side when applicable and at these sites.
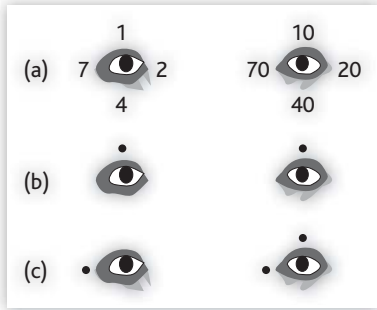
Figure 5.8 A common method of coding information, such as the animal's identification number, can be achieved by using two strings of numbers arranged around an animal's eyes. For example, imagine that an eye has four sides. If the sides on the left eye represent the values 1, 2, 4, and 7 (clockwise, from 1 at the top of the eye) and those of the right eye represent the values 10, 20, 40, and 70, as shown in (a), then it is possible to identify individually up to 154 individuals. What, then, are the numerical codes of the animals illustrated here?

position will allow a unique number to be given to as many as 154 different individuals (**Fig. 5.8**). A similar principle can be used when tattooing an animal's knuckles or digits, removing digits, or using notching (see **section 5.5** and **Fig. 5.9**).

Which methods have been successful with the target species?

Despite all of the factors that we have considered so far, the most common reason for choice
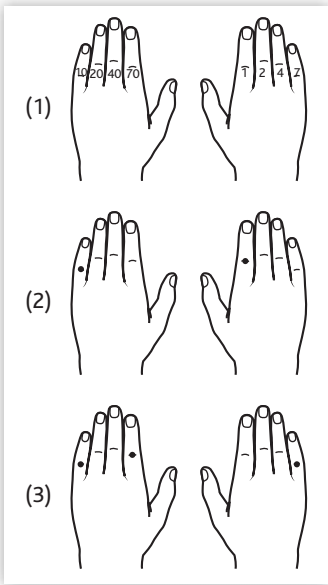
Figure 5.9 The coding system illustrated in **Fig. 5.8** can also be applied by ascribing values to digits or limbs, as shown here.

of method is tradition—the method has been used before with that species and no deleterious signs have been noted by keepers. **Table 5.4** summarizes some of the diverse artificial individual identification methods that are used across the different vertebrate **taxa**. Few documents exist

Method	Fish	Amphibians	Reptiles	Birds	Mammals
Branding	✓		✓		✓
Tattoo	✓		✓		✓
ID cuts			✓		✓ (Ear/horn notching)
Microchips, transponders	✓	✓	✓	✓	✓
Tags				✓	✓
Beads	✓	✓	✓		
Rings/bands/collars			✓	✓	✓
Coat (fur/feathers) clipping	✗	✗	✗	✓ (Toenail clipping)	✓
Dye	✗	✗	✓	✓	✓

Table 5.4 A summary of the suitability of artificial individual identification methods for different vertebrate groups

which provide guidance on different identification methods. However, a helpful exception was written by Beausoleil *et al.* (2004), which considers different methods which can be used to mark New Zealand wildlife. The scope of this document is broad, and it considers some of the main topics.

What degree of security (reliability) is acceptable?

There is an obvious expectation that if an individual identification method is applied to an animal, then its identity will be known. In general, permanent methods of individual identification are considered to be more reliable than their temporary counterparts. But we also need to consider the security of the method chosen: can it be removed, changed, or replaced? If the answer is 'yes', then the safety of the animal's identify is at risk, so that if it were stolen, it could be untraceable. In addition, an animal's identification can also be in jeopardy if an identifying feature is lost and the animal is held in a large social group within which visual differences between individuals are minimal.

The IUCN recommends that all endangered animals are individually identified, as much to safeguard them, as to 'know' who they are. **Exotic animals**, whether endangered or not, are valuable to wildlife trade. Even if these animals are found and confiscated, if they do not have verifiable identification, their ownership cannot easily be assigned. Sometimes, at least in the UK, informally matching reports of lost animals from a zoo with animals that are available for sale can ensure that animals are returned safely. However, if the animals are exported illegally, their origins can become far less clear-cut.

Unfortunately, even those methods of identification that seem to be permanent and tamper-proof can still be changed if the need is great enough. For example, transponder readers can be purchased by animal dealers operating illegally and the original transponders can be removed or replaced with new ones, brands and tattoos can be disfigured to disguise the original mark, and so on. Because of this, more than one method of identification is sometimes used for some animals.

5.4 Temporary artificial methods of individual identification

Many of the methods of identifying individual animals rely on the temporary addition of something to alter the animal's visual appearance, and we can refer to these as adornments. They include such things as tags, beads, rings, collars, or necklaces, and they are most commonly attached to the animal's legs, wings, flippers, or ears, or around the neck. The availability and use of adornments in the zoo industry is led by agriculture, field ecology, and companion animal sectors. Usually, the type and position of adornments is determined by each zoo depending on the animal management system it has in place, although, as mentioned above (see **5.3.2**), there are national or international standards for some species. We can also include transponders in this section because, although they are not visible, they are nevertheless additions to the animal that do not involve permanent changes to the animal's appearance (these sorts of change are considered in **section 5.5**).

Bearing in mind the framework outlined in **section 5.3**, let us now consider the advantages and disadvantages, and hence the suitability, of these different methods.

5.4.1 Rings, collars, and necklaces

Rings, collars, and necklaces are the most benign of adornments, because the animal simply wears them. Of course, the animal needs to be caught and restrained so that the adornment can be secured (see **Plate 5.1(a)**).

Four main types of ring are available.

• Closed rings (**Fig. 5.10a**) are slipped over the foot of a young bird with the intention that they will be permanent and never be removed. Because the longevity of these rings is high, they are a preferred option, but care needs to be taken to ensure that the ring is big enough that it does not become restrictive once the bird grows to its adult size. In addition, these rings can be

Figure 5.10 Various types of ring can be used to identify animals individually—most notably in birds, but also in bats. (a) A closed ring, here illustrated on a Dalmatian pelican *Pelecanus crispus*. (b) A flexible ring, shown here on an inca tern *Larosterna inca*. (c) A metal ring, here shown on a hammerkop *Scopus umbretta*. (Photographs: (a) Paignton Zoo Environmental Park; (b) Kirsten Pullen; (c) anonymous)

difficult to remove if the bird injures itself and its leg becomes swollen, or if the ring gets caught on something within the bird's enclosure.

- Split rings are flexible (**Fig. 5.10b**), so they can be put onto an animal's leg at any age. These rings are not necessarily very secure because, depending on the material from which they are made and whether they adequately fit the leg, they can be bitten off or may fall off. Thus, they may have a reduced longevity and this might require the animal being recaptured and another ring secured.

- Metal rings (**Fig. 5.10c**) are similar to split rings, but are secured in place with pinchers (sometimes call 'ringing pliers'). The application of these requires a skilled professional, because the animal's limb could potentially be damaged when fixing the ring. Metal rings are usually used in long-lived species (for example, on penguins' flippers and cranes' legs) because the rings should be relatively permanent. Unfortunately, over time, the metal can become worn from the animal's movements, and wear and tear to the metal can lead to it becoming sharp, which can then lead to injuries.

- With technological advances, new materials are being used to make rings. For example, a collaborative design team from Bristol Zoo and the University of Bristol has created a new silicone ring which is designed specifically for ease of application, because it can be stretched onto the penguin's flipper or bird's wing. The robust material should withstand extremes in temperature and movement, and so should be long-lasting, without the associated disadvantage of degradation seen in metal. It should thus also avoid injuries to the bird (**Fig. 5.11**).

5.4.2 Beads and ear tags

Beads and ear tags require that the animal's skin is perforated so that the identifying feature can be fixed to its body, so they should be attached by a skilled professional. Best practice requires antiseptic be used at the puncture site to prevent infection and a local analgesic be used wherever practicable. Practically it can take some minutes for a local anaesthetic to become effective so that
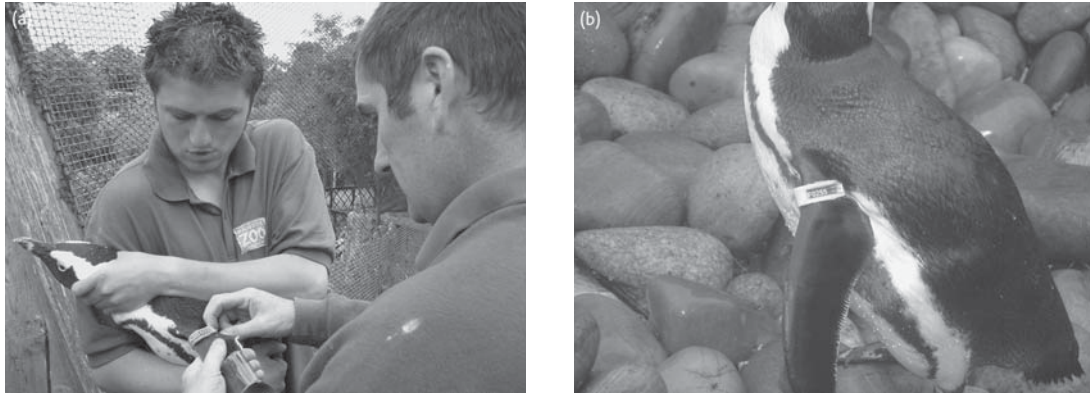
Figure 5.11 Bristol Zoo Gardens, in collaboration with the University of Bristol, designed these silicone composite flipper bands, seen here being applied to African penguins *Spheniscus demersus* at Bristol Zoo. These bands were awarded the 2006 UFAW Wild Animal Welfare Award. (Photographs: Bristol Zoo Gardens)

the site becomes numb; as a consequence the animal has be continually restrained, or released and recaptured. Both these processes are likely to compromise welfare. Thus, it is necessary to consider the likelihood of pain and distress from the procedure which is performed quickly, versus pain relief. An alternative to both of these is to train animals for procedures, so that the potential distress of capture and restraint are removed (see **sections 4.1.2 and 13.4**).

Tags

Tags come in a variety of shapes, sizes, and colours. Tags are routinely used in the ears of mammals, mostly **ungulates**, but are also used in bird wings and the appendages of other kinds of animal. Mammals are usually tagged when young—sometimes, when they are as young as one or two days old—but in other taxa tags may be applied at any age. If the animal is very young, care needs to be taken regarding potential aggression from the mother, and the effects of restraint, separation, and time away from the herd or mother need to be considered. It is also important to position the tag correctly, to avoid major veins and cartilaginous tissue, and to prevent excessive damage. In some situations, ear tagging has been known to cause the ear to collapse permanently.

Inserting an ear tag is probably a painful event for the animal, because it involves puncturing the

ear so that the tag can be threaded through. Ear tags can also pose some problems in the daily lives of animals, because they can potentially be torn from an animal's ear (**Fig. 5.12**), either by getting caught on enclosure furnishings or during social events. Appropriate housing and husbandry should minimize these types of incident, for example by housing socially compatible animals, using well-maintained fencing, and eliminating protrusions into the enclosure. Nevertheless, once an ear tag has been dislodged, it needs to be replaced. An additional problem, which is associated with any identification method that leaves a

Figure 5.12 Two ear tags have been used to identify this mara *Dolichotis patagonum*, but note that there is some damage to the ear. Sometimes, tags can be torn from the animal's ears during aggressive interactions. (Photograph: Vicky Melfi)

wound, is the potential for infection. In US cattle farms, parasitic infection of ear-tag sites has been recognized as a large economic problem that also has deleterious effects on the cattle's behaviour and welfare (Byford *et al*. 1992). This has led to the development of various insecticide-impregnated ear tags, which have varied success (e.g. Anziani *et al*. 2000). While this is an agricultural example, it demonstrates how important it is, in other situations as well, to keep any wound site clean and to monitor it for infection.

In the UK, all bovids need to have ear tags distributed by Defra, and these are part of the animal's 'passport' which ensures that individuals can be monitored and their movements traced. Each animal is given a unique number, combining a prefix representing the zoo and a unique suffix for the individual. Big yellow ear tags are worn in both ears in bovids, and each part of the tag (back and front; four pieces in total for the two tags) is stamped with the individual's identification number.

Beads

Threading beads through the skin of reptiles and amphibians is also undertaken as a means of individually identifying animals (e.g. Rodda *et al*. 1988). In much the same way that coloured leg rings are used in birds, combinations of different coloured beads are used to code different individuals (**Fig. 5.13**). We have already mentioned (see **section 5.3.2**) how birds can develop preferences for sexual partners with particular colours of leg ring, and it is possible that similar preferences for beads may occur in reptiles. It has been suggested that some colours, especially red, should be avoided when using coloured beads with iguanas, because adult iguanas are attracted to this colour and may aggravate the bead site.

5.4.3 Microchips or transponders

The most invasive kind of adornment is the **passive integrated transponder (PIT)**, also referred to as a 'microchip' or simply as a 'transponder' (or, sometimes, a 'PIT tag'). These contain a unique magnetic code and a virtually unlimited number of codes are

Figure 5.13 Individual identification of reptiles is commonly achieved by fixing coloured beads to their dorsal crest. In this example, a green bead has been used to identify individually this Grand Cayman iguana *Cyclura nubila*. (Photograph: Vicky Melfi)

available. The transponder is injected just underneath the skin and usually only requires tissue glue, or one or two stitches, to secure the site. Technological advances have enabled even tiny animals such as dormice to have internal transponders (e.g. Bertolino *et al*. 2001) (**Fig. 5.14**).

Unlike conventional adornments, which aim to provide a highly visible feature to enable individual recognition, the unique numerical code within the transponder can only be identified using a 'reader'. This is a battery-powered handheld device which, when moved close to the site of the transponder, provides a reading of its unique code. In fact, active transponders are also available; these have a battery unit and are able to broadcast information that can be picked up some distance from the animal carrying the transponder (termed radio-telemetry). Since the 1960s, this latter system has been considered useful in the study of animals, and has subsequently been used to study both wild and captive animals (e.g. Essler and Folkjun 1961; Swain *et al*. 2003).

Disadvantages with the use of transponders include the need for most animals to be sedated or anaesthetized so that the transponder can be inserted (see **section 11.6.3** for more on sedation), and the fact that they do not provide a means of identifying an animal that is not 'in the keeper's hands', or in very close proximity to the keeper. Currently, the readers necessary to identify transponder numbers can only be used when the
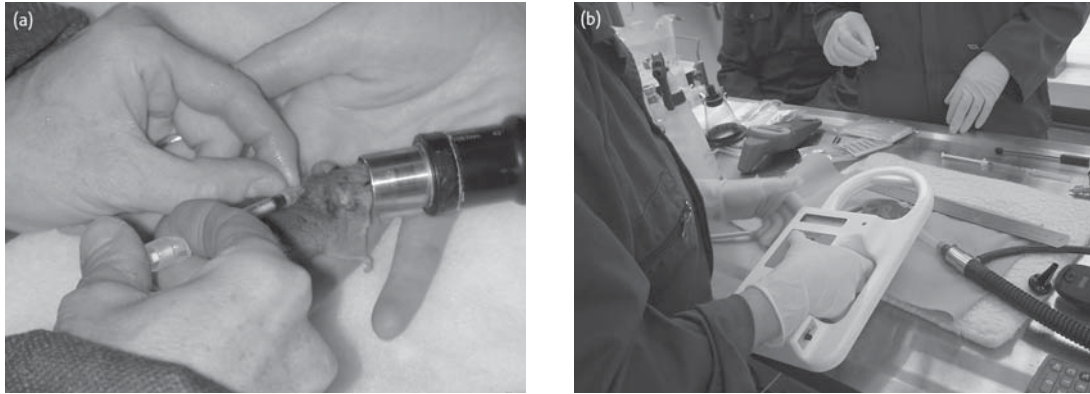
Figure 5.14 (a) Despite their small size, transponders can nevertheless be fitted to small animals, such as this common dormouse *Muscardinus avellanarius*. All transponders should be checked with a reader (b), to ensure that they are working properly. (Photographs: Paignton Zoo Environmental Park)

animal is very close to the reader (indeed, sometimes the reader has to be in contact with the animal's skin) and therefore also close to the keepers. But transponder technology is always moving forward, aiming to increase the distance from which the reader can read the transponder in the animal. For example, recent developments have enabled the individual food intake of domestic cattle to be determined by the animal's unique transponder number. As the cow enters a stall, its transponder is read and the appropriate ration of feed is released from the hopper (e.g. Sowell *et al.* 1998; Schwartzkopf-Genswein *et al.* 1999). Unfortunately, however, the creation of readers that can identify transponders in animals while they are still in their paddocks is probably still some way off.

An additional disadvantage at present is that several companies produce transponders that can only be read by compatible readers. In practical terms, this can mean that a zoo needs several readers to locate and read the transponders of all of the animals in its collection. Again, however, technology is advancing, and 'universal' readers that will read more than one transponder have recently been developed—but there is usually still a need to have more than one reader.

The final disadvantage is that, despite being secured subcutaneously and therefore not likely to get lost, transponders can, indeed, do so. They can be groomed out, because they are placed very near the skin surface and social groomers often take a lot of interest in recent incision sites. But they can also migrate around the body internally (as mentioned above). Some companies that make transponders are aiming to reduce the likelihood of migration by making them with a coating that binds to the animal's skin after implantation.

Although there are limitations associated with using transponders, the technology behind them is constantly improving, and they do outperform other temporary measures for longevity and security. Because of this, transponders are usually used alongside other temporary methods of animal identification which provide a visual cue, such as the ear tags or leg rings described earlier.

5.5 Permanent artificial methods of individual identification

All permanent artificial methods used to identify animals individually change the animal's physical appearance by damaging its body and therefore are referred to as 'mutilations'. In theory, making such permanent changes to an animal's appearance is the only certain way of ensuring that it can be identified indefinitely. At the same time, however, we must recognize that these procedures may cause the animal more pain and stress than many of the other recognition methods that we have

mentioned so far, and this should be borne in mind when decisions are made about when they should be used. Fortunately, technological advances in transponder and reader design are improving their performance to the point at which their longevity and reliability may be greater than even permanent changes to the animal's physical appearance.

Permanent changes to an animal's appearance can be achieved in two main ways: by the removal of part of the animal, or by the addition of a noticeable mark. The clarity of these identifying measures is determined largely by how well they were executed initially. As with temporary methods, permanent measures are most helpful if they can be viewed from a distance and are obviously distinct from other marks in other individuals. By their very nature, permanent measures are long-lasting but, unfortunately, their clarity—and thus their efficacy—can alter over time in much the same way as natural visual characteristics (see **section 5.3.1**).

5.5.1 Removal of part of the animal

There are various ways in which the appearance of an animal can be changed by removing some bit of it. The most common is a practice called notching (sometimes termed 'puncture'), which involves making carefully placed holes or marks in the animal's horn, shell, scales, or ears. Notches can be made in the undershells of chelonians, along the ventral scales of reptiles, and in the ears of mammals. The number and/or position of these marks allow the animal to be identified, sometimes using coded information (see 'Codes' in **section 5.3.2**).

Another technique, used in snakes, involves the removal of scales so that the underlying muscle is exposed (Ferner 1979). The removal of sub-caudal, rather than ventral, scales[8] is thought to reduce the risk of injury, because the possibility of penetration into the snake's abdomen is reduced. Scales are removed from the right and left sides, where the first sub-caudal scale is considered to

[8] Both ventral and sub-caudal scales are enlarged scales on the underside of the snake: the ventral under the snake's abdomen; sub-caudal under its tail.
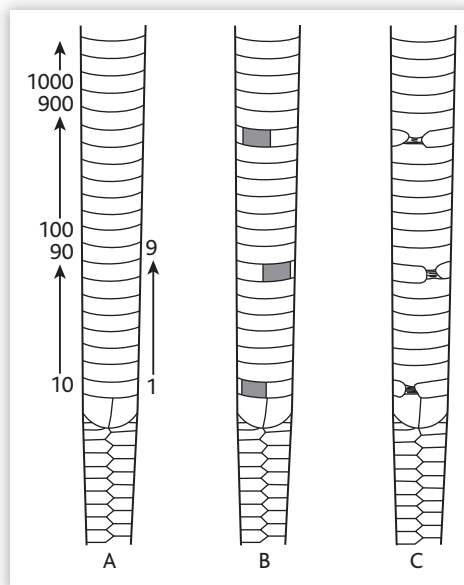
Figure 5.15 One way of identifying individual snakes is to remove a small number of scales, resulting in a unique code. In this example, the numbered code starts from the scale immediately in front of the cloaca (A) so this snake is numbered 819 (B). As the scales heal, the pattern may become less obvious (C).

be the one behind the cloaca. If the second scale on both the right and left sides of the snake were to have been removed, the code would read '2L2R' (**Fig. 5.15**). However, this method has many drawbacks, not least because it is potentially painful and leaves an open wound that may become infected. It is also time-consuming, both to apply, and to read and interpret later, and can lead to ambiguous marks if the scales slowly regenerate or if other injuries occur to disrupt the patterns (Shine *et al.* 1988).

A final method is to remove parts of digits. Toenails can be clipped as a temporary measure (e.g. St Louis *et al.* 1989), but more permanent marking is achieved by removing whole or part of digits (**Fig. 5.9**)—a practice termed toe clipping or digit cutting. This method is sometimes used to identify individual amphibians and reptiles, although it is not used often in zoos. We would expect this to be very stressful for the animals, although, counter-intuitively, there is some evidence that the impact of changing enclosures is more stressful than toe-clipping (Langkilde and Shine 2006).

Of course, this might mean simply that both practices compromise the welfare of the animals.

Unfortunately, even these permanent artificial patterns can deteriorate over time, because other digits can be lost (aside from those purposefully removed), notches can become torn, or additional marks can occur on the animal's horn, shell, or ear. For example, Davis and Ovaska (2001) found that toe regeneration in salamanders *Plethodon vehiculum* meant that toe clipping was lost from 35 weeks onwards.[9] All of this can make the interpretation of these patterns misleading and ambiguous over time.

5.5.2 Branding and tattoos

Branding and tattooing are two popular methods of permanently marking the bodies of animals. In branding, which is widely applied to mark agricultural stock, a shaped metal object known as a 'brand' is rendered either extremely hot or cold and then applied to the animal's skin. Heat branding burns the surface layer of the skin, leaving scar tissue from which hair does not grow and thus a mark is visible. This can be used on a variety of animals; for example, Winne *et al*. (2006) used medical cautery units to heat brand snakes (**Fig. 5.16**). For freeze branding, the area where the brand is to be applied needs to be shaved to expose the skin. Freeze branding destroys the pigment in the animal's hair and thus white hair grows back, characterizing the mark.

Both these processes have been observed to elicit pain responses in mammals (e.g.Watts and Stookey 1999). Freeze branding has also been used in a wide variety of taxa, including crustaceans, fish, amphibians, reptiles, and mammals (e.g. Lewke and Stroud 1974; Fletcher *et al*. 1989; Berge 1990; Measey *et al*. 2001). It is possible that freeze branding leads to slightly less discomfort and pain compared with heat branding, although both processes are associated with a variety of stress- and pain-related behaviours, which are displayed
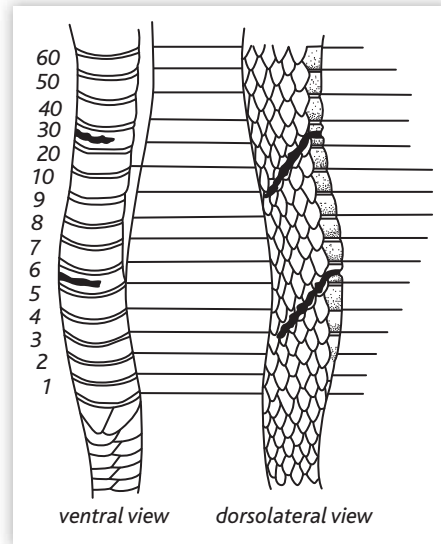
Figure 5.16 Another way of identifying individual snakes is to apply a heat brand to their scales to make a unique mark. As you can see from the illustration, the snake's scales are numbered in a forward direction from the cloaca. In the example we show here, scales 30 and 6 have been branded to identify this individual as #36. (Photograph: Shine *et al* 1988)

both during and after branding. These include the flight response, increased heart rate, vocalizations, and a rise in blood **cortisol** levels (Lay *et al*. 1992; Schwartzkopf-Genswein *et al*. 1997).

In contrast, tattooing works by embedding ink under the surface of the skin via an injection. The tattoos can be applied to various parts of the animal's body, depending on the species and whether or not the mark is expected to be visible. Patterns of tattoo dots are usually used as a visible means of identification, whereby the position and number of the dots is used as a code to identify the animal (see 'Codes' in **section 5.3.2**, and **Fig. 5.8**). Tattoo dots can be placed around the animal's eyes, on its fingers, or wherever there is appropriate skin, such as on the ischial callosities of many Old World monkeys. Alternatively, secluded sites, such as inside lips, ears, or the underside of the animal, may be chosen for the location of the tattoo, because

---

[9] The ability to regenerate lost digits, indeed whole limbs, is widespread in amphibians. Why it is possible in these animals, but not in reptiles, birds, and mammals, is not clear, but it is probably related to their developmental processes (Galis *et al*. 2003).

these usually have little pigment and therefore the tattoo can easily be distinguished.

The usefulness of artificial marks such as these added to an animal's body relies heavily on their clarity, and this, as with all permanent measures, can decline over time as the animal ages and its appearance changes. This can be exaggerated by the position of the mark. For example, tattoos can become hard to read when the skin becomes wrinkled or loose, which is common in ageing animals.

5.6 Record-keeping: what information could, or should, be recorded?

It has been said that you can never collect too much information—but this is not strictly true. Certainly, it would be ideal to keep as much information as possible about each and every individual animal, because the information could then be analysed at the level of the individual and/ or the population. This analysis could be carried out now, or at some time in the future. However, the collection and recording of all this information takes time. Many larger zoos have registrars whose sole responsibility is to manage the zoo's records, but very often time is limited and so we need to consider what is the minimum that needs to be recorded about each animal.

The Secretary of State's Standards of Modern Zoo Practice (SSSMZP) in the UK state:

Individual records must provide:
a) Individual identity and scientific name.
b) Origin (wild or captive born, identity of parents, previous locations).
c) Dates of entry into and disposal from the collection, and to whom.
d) Date, or estimated date, of birth or hatching.
e) Sex (when known).
f) Any distinctive markings (i.e. tattoos, rings, or transponders).
g) Clinical data, including details of, and dates of, treatment given.

h) Behavioural and life history data.
i) Date of death and results of any post-mortem.
j) Any escapes, where to, and any reasons why they occurred; damage or injury caused to, or by, an animal to persons or property; any remedial measures taken to prevent recurrence.
k) food and diets.

(Defra 2012a)

It also requires an inventory, or annual stocklist, for each animal collection. It is expected that records covering the previous six years are kept on site at the zoo and are easily accessible, so that the zoo's local authority can view them.

Therefore the main information needed can be summarized as **life history traits**, daily events, medical information, routine housing and husbandry, and body measurements.

5.6.1 Life history traits

Life history traits are the big events that occur in the life cycle of a zoo animal, such as births, deaths, and transfers between zoos; in captivity the latter is equivalent to forced migrations which occur in wild populations. The amount of detail that can be recorded about these events is largely determined by the record-keeping system implemented (see **section 5.7**), although there are some obvious basic bits of information that are required. When animals are born, it is important to know who their parents are, because information about parentage enables the captive population to be genetically managed. This is not always as easy as it might seem: for example, in some situations it may be difficult to know who the sire (father) is if multiple adult males are present in the group; equally, it may be difficult to know who the dam (mother) is if it is a species within which mothers do not associate with their young after parturition. The dates on which animals are born, moved to other zoos, and die should also be recorded, because this enables the animals to be tracked, which is necessary for disease control and trade prevention. It also permits demographic analyses of the captive population: for example, calculating

how long a species lives in captivity, or whether the population is self-sustaining or is not breeding (see **Chapter 9**). As an example, analyses of records kept on cheetah *Acinonyx jubatus* in US zoos between 1987 and 1991 showed that the population was increasing (from 52 to 72 animals) and that infant mortality had declined from 37 to 28 per cent, although this was still highly variable (Marker-Kraus and Grisham 1993).

5.6.2 Daily events

Unlike life history traits, which are significant events in the animal's life, daily events are observations made of the animal that may, or may not, be of any consequence. For example, what if an animal does not eat one day? Perhaps the animal is ill; alternatively, it might be reproductively active, or might not like the food given to it, or perhaps it found food elsewhere (for example, **carnivores** sometimes catch prey that enters their enclosure), or it could be occupied by something else in its enclosure, or there may be something that the keeper has not even considered. Without the collection of more information on a daily basis, it is impossible to know whether the fact that the animal failed to eat is a problem that needs to be resolved or the consequence of a 'reasonable' event.

Information that may be noted on a daily basis varies, but should probably include any observed deviations in the animal's appearance or changes from its normal behaviour. It is also good practice to note any miscellaneous events that may affect the animal in the future: for example, if any change was made to routine housing and husbandry, such as feeding it later than usual, visitors staying in the zoo late, or the presence of fireworks. By reviewing these daily events, it will be possible to investigate what factors affect the animal's behaviour, health, and reproduction. Patterns may be obvious, as in the above example, or more complicated: for example, a group of animals that will not come in off exhibit several times might be influenced by the behaviour of a neighbouring group of animals.

5.6.3 Medical information

It is obvious that information about the health of animals within the collection needs to be recorded. It is most important that the information is then collated and reviewed to establish whether animals are healthy and the veterinary care given is successful. Medical records are also vital in **preventive medicine** (see **section 11.4**), which involves identifying which animals or species seem to have health problems, which sites within the zoo show a high incidence of disease, and whether the disease is spread through the zoo. As with other forms of record-keeping, the type and detail of medical information kept is largely determined by the record-keeping system used. (See **section 5.7.4** on the Medical Animal Records Keeping System (MedARKS); this will in time be subsumed by ZIMs.)

5.6.4 Routine housing and husbandry

Keeping routine housing and husbandry information is helpful when investigating patterns in animals' behaviour and health, because it is likely that the two are linked. Much housing and husbandry, such as the enclosure in which the animals are kept, the diet given to them, and the basic daily routine (i.e. when animals are fed, moved around their enclosure, etc.) is routine and therefore probably varies very little from day to day. This means that records of housing and husbandry can usually remain unchanged for quite long periods of time, usually until some changes occur such as the introduction of a new diet or modifications being made to the enclosure.

5.6.5 Body measurements

The collection and study of body measurements, such as weights and lengths, is referred to as biometrics or morphometrics. For most taxa, there are standard measurements that are usually taken, and some of these are described and illustrated in **Box 5.2**.

Box 5.2 STANDARD BODY MEASUREMENTS FOR ANIMALS

When taking measurements of animals, the International System of Units (SI units) should be used, so length measurements should be recorded in millimetres or centimetres, and weight recorded in grams or kilograms. A ruler or measuring tape, or string that can later be measured accurately, can be used to determine these lengths. Measurements of small animals, such as many birds, should be taken using callipers, because these are more accurate in this case.

Mammals

There are at least four standard measurements that can be recorded from mammals (**Fig. 5.17a**), as follows.

- *Total length* Measure from the tip of the nose to the front end of the tail vertebrae. If possible, the animal should be placed on its back so that the backbone is straightened, but not stretched. Position the head with the nose extending straight forward in the same plane as the backbone.
- *Tail length* Bend the tail at a right angle to the body and measure the distance from the angle to the far end of the last tail vertebra. Do not include any protruding hairs.
- *Hind foot length* Measure from the back edge of the heel to the tip of the longest toe, excluding the claw (in the USA, the claw is included in this measurement).
- *Ear length* Measure from the notch at the base of the ear to the furthermost point on the edge of the pinna (external ear flap).

Two additional standard measurements can be recorded from bats (**Fig. 5.17b**).

- *Tragus length* The tragus is a leaf-like structure projecting up from the base of the ear in many bats. Measure from the base to the tip.

- *Forearm length* Fold the wing and measure from the outside of the wrist to the outside of the elbow.

Birds

At least five standard measurements can be recorded from birds (**Fig. 5.18**), as follows.

- *Total length* The distance from the tip of the bill to the tip of the longest tail feather (rectrix).
- *Wing length* The distance from the bend of the wing to the tip of the longest primary. The curvature is not straightened and the measurement is made from the bend directly to the tip.
- *Tail length* The distance from the tip of the longest tail feather to the point between the middle feathers at which they emerge from the skin.
- *Tarsus length* The distance from the point of the joint between the tibia and tarsus, to the point of the joint at the base of the middle toe in front.
- *Bill length* This is measured from the tip of the upper mandible in a straight line to the base of the feathers on the forehead. In birds with a cere (the smooth featherless skin between the beak and the forehead) or similar structure, the measurement is made from the front edge of the cere to the tip of the bill.

Amphibians and reptiles

Standard measurements in amphibians and reptiles include the following.

- *Snout–vent length (SVL)* Sometimes referred to as 'total length', this measurement is recorded from the tip of the animal's
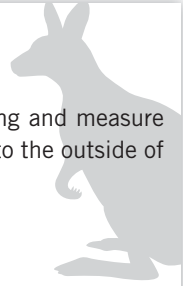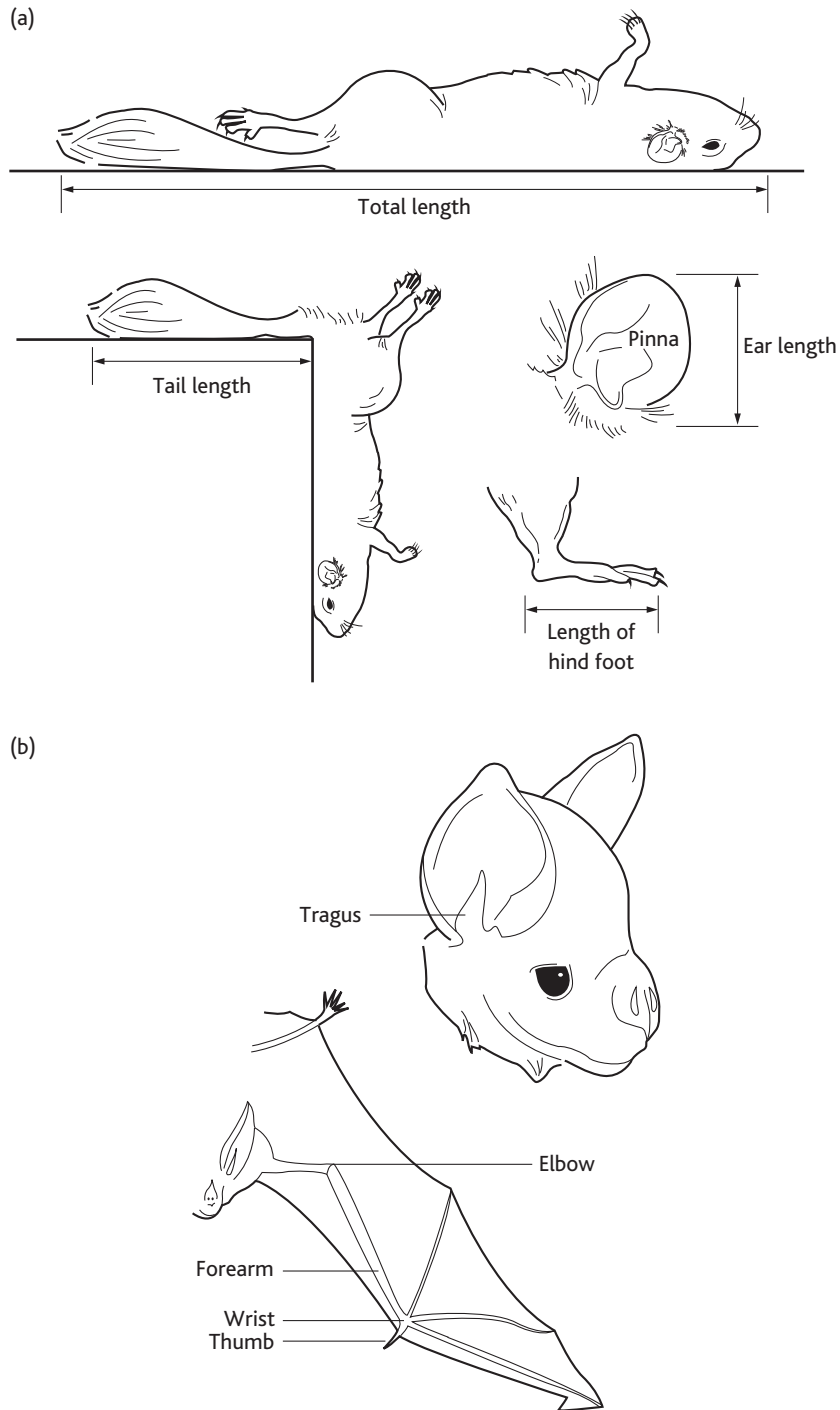
Figure 5.17 (a) Illustration of the standard measurements that can be recorded from a mammal. (b) Two additional measurements can be recorded from bats.

(a)

Total length

Upper mandible (bill)

Primaries

Rectrix
(tail feathers)

Tail length   Tarsus length

(b)

Wing length
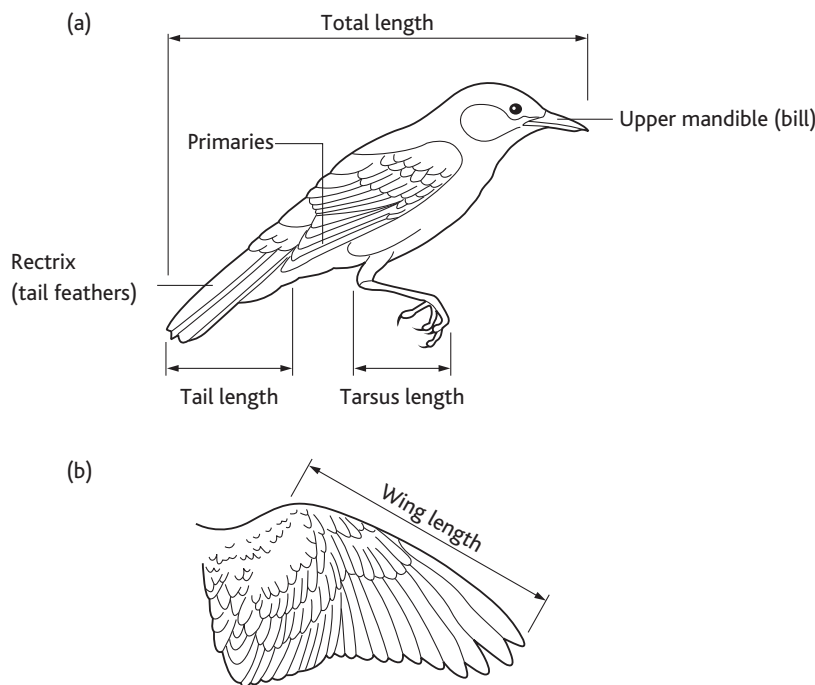
Figure 5.18 An illustration of the standard measurements that can be recorded from a bird.

nose to its cloaca in amphibians, snakes,* lizards, crocodilians, and tuataras. In salamanders and caecilians, total length is measured from the tip of the nose to the tip of tail (SVL can still be recorded).

- *Measures for chelonians*   Different measurements that can be recorded include width of carapace (upper shell), shell height, plastron (lower shell) length, and width.

****Note** Snakes that are artificially stretched can be considerably longer than when they are relaxed. Therefore they should be placed on a soft surface (a towel, a snake bag, etc.) and pressed gently downward, using a piece of transparent material such as Perspex. The outline of the animal is then traced using a soft-tipped pen. Using string, the length is determined from the drawn outline. Alternatively, a novel approach involves photocopying the specimen, preferably in a coiled position. It should be noted that there is a small discrepancy between the size of the actual specimen and the final photocopy, which is around 98 per cent of actual size (Chalmers 2006).

Knowing the body measurements of an animal is essential to ensure that enclosures and travelling crates are an adequate size. Furthermore, the regular collection of these measurements provides additional information that can be used to monitor the health and welfare of the animals. For example, regular weighing can help in an assessment of whether the diet is appropriate, and so inform keepers about the animal's health and whether the animal's weight remains constant, increases, or decreases. Actually weighing an animal on scales should be much more accurate than trying to estimate if it has changed weight simply by looking at it. Andrew Fry, of Paignton Zoo Environmental Park, UK, has commented that monitoring the daily weight gain of pregnant female **callitrichids** has been used as a reliable indication of their expected parturition date. In hand-rearing, daily weight gains are seen as a sign that the process is progressing well and the infant is developing (see **section 9.5.3**). Very often, wild animals gain and lose weight seasonally, as food becomes more or less available. These fluctuations in weight can affect physiological processes,
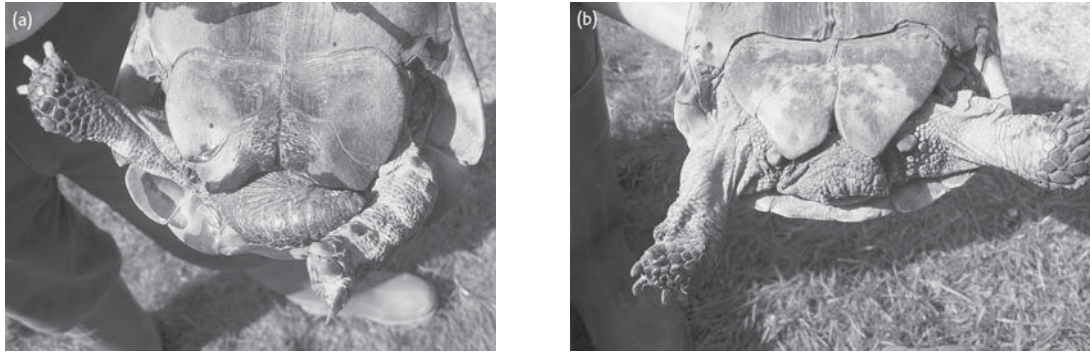
Figure 5.19 Sex determination in turtles cannot be known with complete certainty from body measurements, but a fairly reliable indication can be drawn from a comparison of the tail length, width, and the distance of the cloacal opening down the tail, as in these spur-thighed tortoises *Testudo graeca*. Generally, males (a) have longer tails and the cloacal opening is further down the tail than it is in females (b). (Photographs: Paignton Zoo Environmental Park)

such as reproductive cycles. Therefore it may be prudent for husbandry regimes to mimic the fluctuation in food quality or quantity throughout the year (see **Chapter 12**).

Body measurements can also be helpful for sexing and ageing animals. If data are available from other animals, it is possible to draw growth curves from which estimations of age can be made. For example, the birth dates of young wallaby joeys can be estimated by taking foot measurements and weights (Bach 1998). Birds, reptiles, and amphibians can sometimes be difficult to sex because of their lack of external genitalia, and morphometrics can often help with this. In birds, especially, there is a huge wealth of literature documenting

the use of morphometric values to distinguish the sexes. In many reptiles, as a general rule of thumb, tail length can be used to help identify the sexes. In snakes, for example, males have broader tails than females because of the presence of the retracted hemipenes,[10] whereas in turtles, males have longer tails and the cloacal opening is further down the tail than it is in females (**http://www.chelonia.org**) (**Fig. 5.19**).

More recently, molecular DNA (see **Box 5.3**) sexing techniques have been used to establish

[10] Hemipenes are the paired intromittent sexual organs of snakes and lizards, usually kept inverted in the body when not being used in copulation.

Box 5.3 **DNA: FROM SAMPLING TO INTERPRETATION**

In recent years, advances in molecular genetics have progressed rapidly (see **Box 10.4**). Using these techniques, it is possible to identify animals from most taxa individually with a variety of samples, the majority of which can be collected non-invasively: see, for example, Washio *et al.* (1989) on non-human primates; Ortega *et al.* (2004) on canids; Burke and Bruford (1987) and Taberlet and Bouvet (1991) on birds; Miller (2006) on reptiles and amphibians; Lucentini *et al.* (2006) on fish. Samples that can be used for

this purpose include fins, scales, blood, saliva, cloacal and buccal swabs, semen, faeces, urine, hair, and feathers.

Other measures that benefit captive management and conservation biology, and which can be determined using molecular genetics, include species, subspecies, races, parentage, **effective population** size, sex (for example, in the panda—see Durnin *et al.* (2007)), consumed diet (for example, in the pinniped—see Deagle and Tollit (2007)), and much more (Haig 1998).
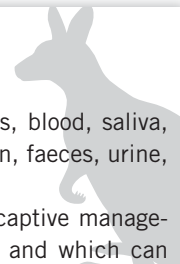
which morphometric values best predict the sex of an individual (Cerit and Avanus 2007). For example, the endangered Pohnpei Micronesian kingfisher *Todiramphus cinnamominus* exhibits reversed sexual dimorphism, in which the male is smaller than the female. But the measurements taken from males and females overlap with each other, so no single measurement reliably indicates sex. If a combination of four indices is used—culmen, tarsus and wing length, and weight (see **Box 5.2** for more information on these measures)—discriminant function analysis[11] is able to assign the sex of a bird correctly in more than 73 per cent of cases (Kesler *et al.* 2006). Similarly, wing chord length and weight measured in redtailed hawks *Buteo jamaicensis calurus* could predict the sex of the bird in over 98 per cent of cases (Donohue and Dufty 2006).

Sizes and weights of animals are often of interest to zoo visitors (**Fig 5.20**). Because of this, some zoos have integrated the process of weighing animals into educational demonstrations. One way of doing this is by connecting a set of animal scales to a large screen that is on display to the public so that, when an animal steps onto the scales, the public can read its weight. When zoos have trained animals to step onto scales, which are placed in their enclosure, many of the problems associated with catching and handling animals, in order to get weights, can be avoided (Savastano *et al.* 2003).

5.6.6 Establishing 'normal' values

To monitor and evaluate the health and welfare of zoo animals effectively, it is necessary to have an idea of what measurements are 'normal'. By 'normal', all we mean is the range of values observed in members of a species of the same sex and age which do not have any **pathology**. Analysis of pooled data—collected over several years, or from several zoos, or both—can be helpful in calculating the mean, median, mode, and standard deviations for a given parameter. For example, data recorded on captive Arabian oryx *Oryx leucoryx* between June 1986 and April 1992 led to the calculation of various reproductive parameters, including oestrous cycle length (22 days), gestation period (260 $\pm$ 5.5 days), inter-birth interval (295 $\pm$ 42 days), and mean calf weight (6.5 $\pm$ 0.7 kg) (Vié 1996).

How reliable these 'normal' values are depends on the size of the data set, because the larger the body of information is from which calculations are made, the more accurate the results will be. Therefore zoo records are important not only in the monitoring of an individual animal in a particular zoo, but also in the monitoring of the captive population in general and of other individuals in other zoos.

Figure 5.20 Gaining weights and measures from animals in captivity might seem like a easy task, but there can be logistical issues with some species held. In this situation the walrus at the Dolfinarium Harderwijk are trained to get onto scales to obtain regular weights. (Photograph: Katharina Herrmann)

5.7 Zoo record-keeping systems

As we have seen, the main aim of keeping records is to use the information contained within them to monitor individuals and populations of animals.

[11] Discriminant function analysis is a multivariate statistical technique that is used to determine which of a large number of variables is most successful in classifying objects, or animals, or behaviours (or anything else that can be measured through a number of variables) into groups.

Therefore it is essential that the record-keeping system used should facilitate inspection and analyses of information, so that the health and welfare of individuals can be regularly assessed and maintained to a high standard. Indeed, the SSSMZP (Defra 2012a) expect that zoo records should be kept and filed in such a way that they are easily accessible.

Records can be kept either in a paper format or electronically, and there are advantages and disadvantages associated with both methods. Paper is cheap and low-tech, and there is no restriction about who is able to collect and record information in this way. But paper records are easily lost and damaged. In addition, the collation, organization, and storage of a paper record-keeping system is extremely laborious compared with how easily a computer software package can undertake a similar task.

Computer programs also have their limitations, however. As a high-tech alternative to paper record-keeping systems, computer-based systems are more expensive to operate and maintain, and they require staff who are specifically trained to use the software. Despite this, they are certainly the easiest method of cataloguing, retrieving, and comparing information, especially for large collections and between collections (for example, in the calculation of 'normals'—see **section 5.6.6**).

Given that there are merits associated with both systems, many zoos use a combination of paper-based and electronic record-keeping systems. For example, daily events will probably be recorded by keepers in paper diaries kept close to where they work, whereas less frequently collected information—such as life history, and housing and husbandry data—will be entered into an electronic system. Paper records can always be transcribed into an electronic form at a later date.

Although there are different computer software programs available for zoo record-keeping, most zoos use those that have been formulated by the International Species Information System (ISIS).

5.7.1 The International Species Information System (ISIS)

ISIS is a non-profit organization that was established by Dr Ulysses Seal and Dr Dale Makey in 1973 (Flesness 2003). They believed that a global database of zoo animal records was necessary to achieve long-term conservation goals. The database started with the records of fifty-one zoos in Europe and the USA, and now represents almost 850 professional animal collections in over eighty countries on six continents, with records for over 2.5 million animals of about 15,000 species (Laurie Bingaham-Lackey, personal communication). It should be noted that since the publication of the first edition of this book, about 200 professional animal collections have joined ISIS, and more fish and invertebrates have been added to the database. Interestingly, plants are now included too! By using ISIS software, records can be kept in a format that can be readily uploaded into this ISIS central database. The global database is an invaluable resource, because it provides security—a back-up for records from individual zoos—and it also enables the comparison of information between zoos. The exercise of establishing 'normals' (see **section 5.6.6**) is much easier when the data are already available in a central database and represent large numbers of animals in many different zoos. Thus, these data sets are a valuable resource for zoo research, especially epidemiological studies, and investigations of captive breeding and population management (e.g. Boakes *et al.* 2006; Young et al. 2012). Recently, access to the ISIS database has been restricted to ISIS members only, but researchers can make an application to ISIS for access specific to their study needs; researchers can also contact **studbook** keepers and collaborate with them (**Fig. 5.21**).

ISIS has recently rolled out new web-based software computer programs for managing living collections—Zoological Information Management Systems (ZIMS) (**Fig. 5.22**). It will take some time for ZIMS to be rolled out to all ISIS members, so we will first provide an overview of its precursor programs, Animal Records Keeping System (ARKs), the Single Population Analysis and Records
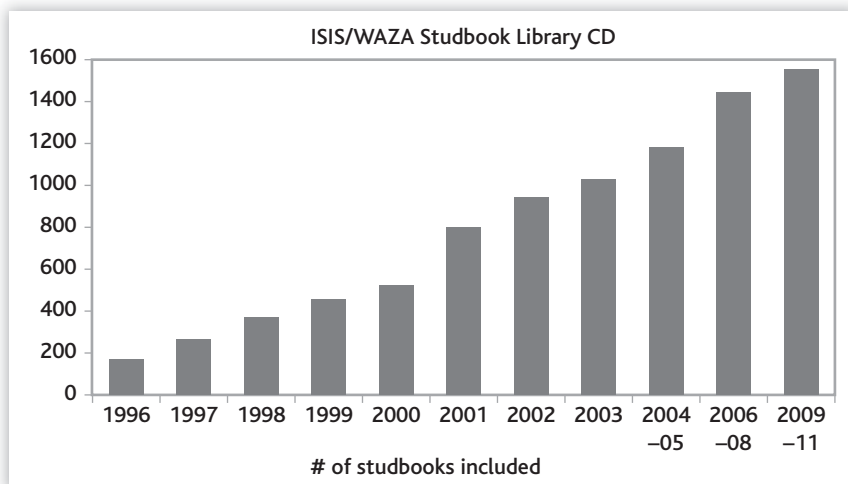
Figure 5.21 Annually, ISIS publishes a studbook CD representing its members activities (99% of all published studbooks). As of 31 July 2011 this comprised 1,350 regional and 190 international studbooks and 292 husbandry manuals. (ISIS/WAZA 2009–11)

Figure 5.22 ZIMS represents a pioneering software package which, it is hoped, will revolutionize record keeping and managing captive populations (ISIS 2010)

Keeping System (SPARKS), and MedARKS, as these are still in use in many institutions.

5.7.2 The Animal Records Keeping System (ARKS)

ARKS is a computer program created to manage all the types of information that can be recorded about zoo animals which were described in

section **5.6**. Within the system, there are some basic fields that have to be completed for each animal; required fields include information such as species, date of birth, birth origin, sire, and dam. There are also additional optional fields, which can be completed at the discretion of the registrar or whoever is entering the information; for example, descriptions of identifying features, reproductive notes, information from daily report sheets or about the enclosure, or in fact anything that the registrar feels will be helpful in the future and thus worth noting. It is a legal requirement to keep certain details about animals maintained in zoos (see **section 5.6**), but, as we have already discussed, the collation of as much information as possible is important as it greatly increases our knowledge of the animal and enables us to explore aspects of its life history in captivity more fully.

Information can be exported or printed out from ARKS for one individual or for a group of animals. ISIS programs were initially biased towards the recording and analysis of data from mammals, but ZIMS (as well as supplementary programs, such as EGGS[12]) provides a

---

[12] EGGS is not an acronym, but rather the title of the program which records information on egg production, incubation periods, **fertility**, hatchability, egg weights, and measurements for breeding and management purposes.
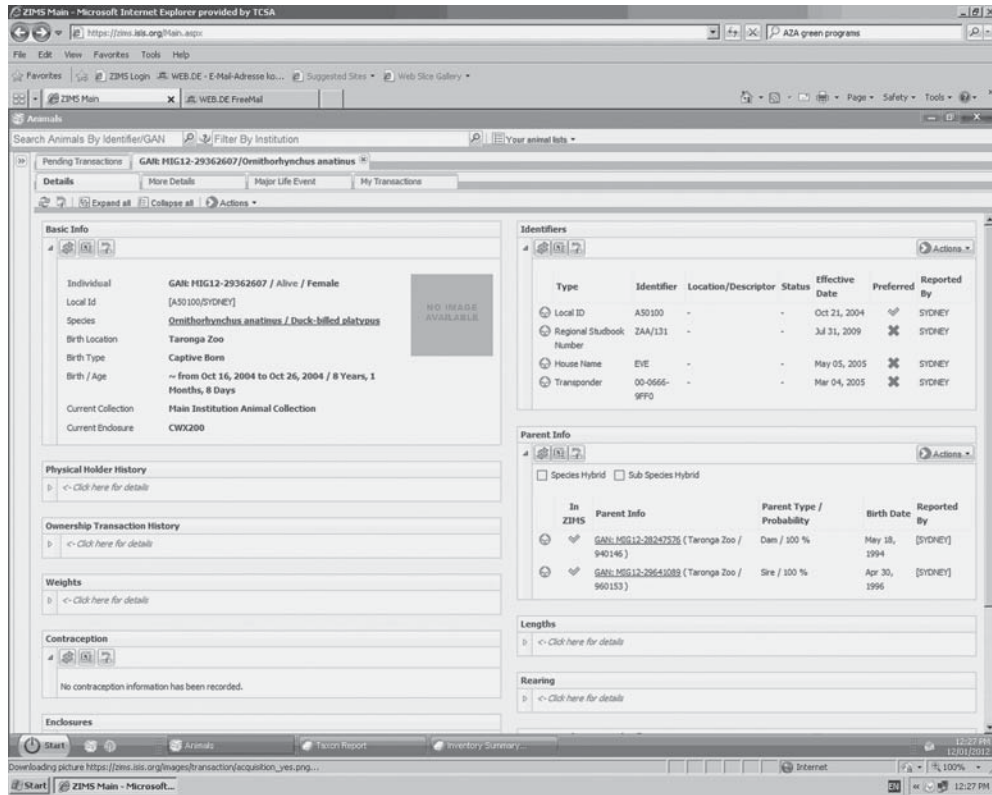
Figure 5.23 ZIMS provides the opportunity to record lots of information about the animals (or plants) in your living collection, as well as information about life support systems and much more. In this platypus record, you can see information that has been entered about her date of birth and what measures are used to identify her individually, as well as her parentage (Photograph: Taronga Conservation Society Australia)

flexible platform to collate data on many different species (**Fig 5.23**).

5.7.3 The Single Population Analysis and Records Keeping System (SPARKS) and PMx

SPARKS was designed to facilitate the work of studbook keepers in managing small captive populations of animals (see **Chapter 9** on 'Small Population Management'). Like ARKS, the program stores information about the life histories and events of individually identifiable animals, but these are collated by species. However, its real purpose is to analyse these data by performing basic demographic and genetic analyses, which can be achieved through SPARKS

or, alternatively, exported and analysed in PMx. PMx[13] is the successor to the software program Population Management 2000 (PM2000). Although the two programs are complementary (data cannot be stored in PMx), PMx is a far more sophisticated tool for managing the demographic and genetic qualities of small captive populations than SPARKS. It is usual that data are stored in SPARKS, in which basic demographic and genetic analyses performed; for example, calculation and display of population size, growth rate, sex–age pyramid, and fecundity and mortality parameters, as well as inbreeding coefficients

[13] PMx was designed by a small team, with input from the global zoo profession, and though the program is copyright, it is distributed freely to users.
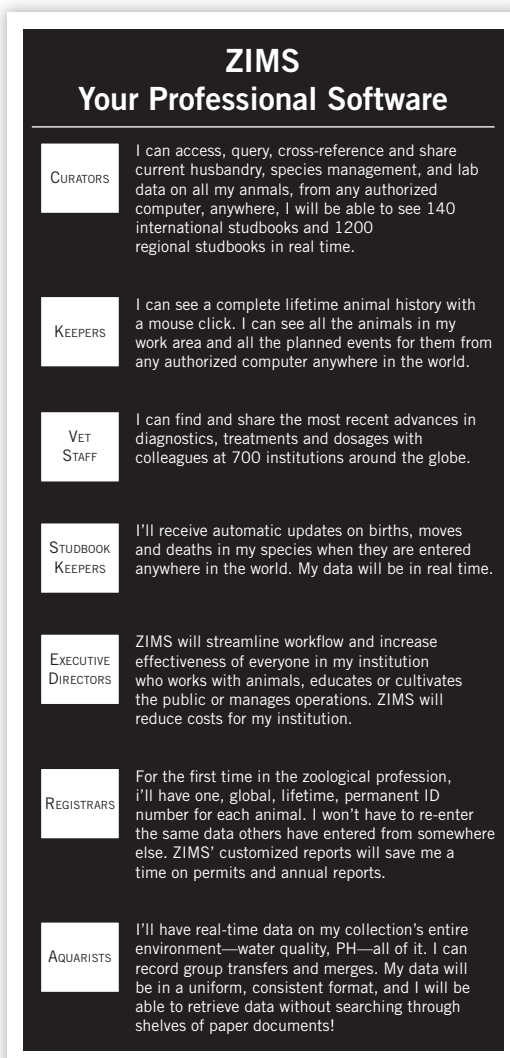
for proposed pairings. However, PMx offers the opportunity to calculate these and other variables, as well as to model potential outcomes for possible management decisions; for example, potential pairings, introduction of founders, increasing generation length, and much more (Ballou *et al.* 2011; Traylor-Holtzer 2011). Various manuals and guidelines have been published to help with data entry and analyses (Wilcken and Lees 1998; Wiese *et al.* 2003; ISIS 2004; Leus 2006).

5.7.4 The Medical Animal Records Keeping System (MedARKS)

MedARKS was designed specifically to record **clinical** and pathological information about individually identified animals. This information, once shared with the global database, facilitates the estimations of 'normals', and thus helps zoo managers and vets to assess the health and welfare of their animals.

5.7.5 Zoological Information Management Systems (ZIMS): it's here!

Previously, all ISIS computer software packages have worked independently of each other, which has meant that the same data needed to be entered into each program separately (**Fig 5.24**). Thus, for example, the birth of an animal needs to be entered not only into the ARKS program of the zoo holding it, but also into the SPARKS program of the studbook holder and the MedARKS program of the vet monitoring the animal. What is worse, if the animal is transferred to another zoo, the new zoo will also need to input all the animal's data into their ARKS program. There is an obvious duplication of effort here, but, more worryingly, there is an increased potential for errors; each time that data are re-entered into a different program, there is the possibility that a mistake will be made and that the information will no longer match the information current in other software programs. Furthermore, as data entry relies on the time of someone to enter the data, there is often a time delay between the event occurring

Figure 5.24 ZIMS can, and should, be used by different zoo professionals who have an active role in the captive management of individuals and populations. (ISIS 2010)

and it being present in the records; and often a birth may be recorded in one system and not in another. In summary, a lot of work and confusion can occur.

Thankfully, this worry is becoming a thing of the past. Zoological Information Management Systems (ZIMS) is the newest computer software package to be designed by ISIS and aims to integrate all the previous programs into one global Internet-based database. This means that information will only need to be entered into the database

once, in real time, thus reducing the likelihood that errors will be generated. Zoo professionals who need access to information will be able to review zoo records as they did previously, but with additional program features allowing greater analyses of data for population management or epidemiological analyses.

ZIMS is certainly ambitious, and because it has so much to accomplish and because there will be a large amount of data being transferred and training required for many different zoo professionals, the program is being released in bite-size chunks. Initially, zoos are receiving the software which will replace ARKs, and will maintain records about the animals, enclosures, life support, and a variety of other features, enabling aquarists to monitor water quality, registrars to assign one fixed ID number to an animal for its lifetime, and more (**Fig 5.25**). The second release will subsume SPARKs and allow studbook keepers to maintain their studbooks in real time, and the third release
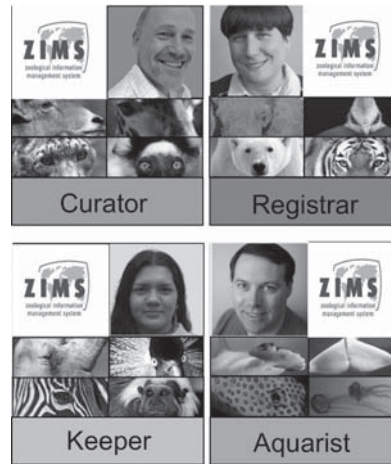
Figure 5.25 Unlike previous captive management software, ZIMS is all about integration, and is as applicable to the management of fish, as it is to mammals and insects. (ISIS 2010)

will replace MedARKs. This software has been designed by the zoo profession, and so there remains some flexibility in how to use and operate it.

Summary

• The identification of individual animals is essential in a zoo collection, so that they can be monitored, information recorded, and records kept that can be reviewed and analysed.

• Although record-keeping may sound a little stale, it is what underpins knowledge of zoo animals, and thus should inform all our decisions about the animal's daily life and long-term position within the captive population.

• The analysis of zoo records promises a wealth of information that can further inform our knowledge of species, their breeding, mortality, and health, and the impact of our housing and husbandry regimes. In short, being able to recognize individuals is vital, and keeping good records about those individuals is the cornerstone of good animal management.

• ZIMS is set to be a pioneering program enabling many different zoo professionals to better look after the daily lives of individual animals and the lifetimes of populations.

Questions and topics for further discussion

1. How might you individually identify an animal, using natural visual characteristics?
2. Name four different artificial methods of individually identifying animals, listing the advantages and disadvantages of each.
3. Should permanent methods of individual animal identification be used? Justify your conclusion.
4. What is ISIS and what does it provide for the zoo community?
5. Who will ZIMS appeal to and why?
6. Identify two demographic and three genetic details that you can discover about a captive population using SPARKS and/or PMx.

Further reading

Most of the material that we have covered in this chapter is a distillation of accepted practice[14] within the zoo community, together with appropriate references to journal articles where these are available. There is a useful section (Appendix 2) on animal identification and marking techniques in the second edition of Kleiman *et al.*'s book, *Wild Mammals in Captivity: Principles and Techniques* (Kalk and Rice 2010). Beausoleil *et al.* (2004) also provide a broad overview of different marking methods which can be applied to various taxa including amphibians, reptiles, and marine mammals. The reader is referred to general statistics textbooks for an explanation of terms such as mean, median, and standard deviation. *Biomeasurement* (Hawkins 2009) is a good starting point.

Websites and other resources

The are many different manufacturers that make identification tags for animals. A website that is particularly useful is that of Dalton Rototags (**http://www.dalton.co.uk**). Dalton produces a range of tags from the 'Minitag' to the 'JumboTag'. These are suitable for many different species and are widely used for tagging livestock in the UK, as well as for wild animals from rabbits to seals (e.g. Testa and Rothery 1992). Other tag manufacturers in the UK include Allflex (**http://www.allflex.co.uk**) and Fearing (**http://www.fearing.co.uk**). The online catalogues of all three of these companies include advice on best practice during tagging. In the USA, Biomark (**http://www.biomark.com**) is a well-established provider of animal identification tags. The ISIS website (**http://www.isis.org**) contains a wealth of information, including listings of zoos in which different animal species are held and presentations on the new ZIMS software.

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.
http://www.oxfordtextbooks.co.uk/orc/hosey2e/

---

[14] Some of the array of animal marking methods reviewed are rarely practised (e.g. wing tagging in birds and scale removal in reptiles), but there is no current regulation to prohibit them.

Chapter 6
Housing and husbandry

This chapter is about the accommodation and day-to-day maintenance of animals in **zoos**. Housing and husbandry regimes have to meet the needs of many stakeholders: principally, the animals themselves, their keepers, and the zoo visitors. We will start by outlining the needs of these different stakeholders, and the demands that they place on zoo animal housing and husbandry. Within the construction of zoo animal housing, trends are apparent that reflect the differing popularity of enclosure styles over time. An overview of some of the most prominent housing styles is provided, and their merits and drawbacks are discussed in terms of how they meet the needs of different stakeholders. The development of good housing and husbandry regimes requires many variables to be balanced against one another, ranging from financial constraints, the reproductive status of individual animals, or sourcing building materials from sustainable resources, through to things such as ensuring the comfort of visitors while viewing animals in poor weather.

   Deciding which of the various housing and husbandry alternatives should be implemented can be determined using a number of criteria. However, what is essential is that an evidence-based framework is adopted so that different elements of housing and husbandry can be systematically evaluated. This theme is woven throughout this book, and in this chapter we detail what is meant by evidence-based zoo animal management.

   The following key issues relating to zoo housing and husbandry regimes and implementation are highlighted in this chapter.

   6.1   The needs of many
   6.2   Advances in enclosure design
   6.3   Husbandry from birth to death
   6.4   Studying how housing and husbandry affects captive animals
   6.5   Guidelines and housing and husbandry recommendations

In addition, there are boxes that describe evidence-based zoo animal management, examine in more detail the related issue of whether it is the physical space itself or the complexity of that space that is of more importance to animals, and also examine the technique of **post-occupancy evaluation (POE)** which can tell us about how that space is being used.

6.1 The needs of many

Enclosure design and good husbandry have developed to incorporate the requirements and needs of many stakeholders, but there are three principal groups whose needs should be considered when designing zoo housing and husbandry regimes:

(1) the animals, to ensure that they have good welfare and that they form self-sustaining populations;

(2) the keepers, so that they can adequately care for the animals;

(3) the zoo visitors, who want to enjoy their visit to the zoo and whom zoos want to educate about conservation and the environment.

6.1.1 Animals' needs

At the very least housing and husbandry should provide animals with the facilities and opportunities to ensure that the **five freedoms** are fulfilled (FAWC 2012) (see **Chapter 7**). Different species have evolved to exploit different environmental niches, so there is no 'one size fits all' rule to housing and husbandry that will meet the needs of the whole diversity of species held in zoos. To illustrate this, consider species such as the black rhinoceros *Diceros bicornis* and the Toco toucan *Ramphastos toco*, between which the species differences may be visually obvious, but which may, in fact, both suffer from a similar nutritional problem—iron storage disease (see **section 12.8.1**). In contrast, species such as the pig-tailed macaque *Macaca nemestrina* and the stump-tailed macaque *Macaca arctoides* look visually similar, but while providing **enrichment**, in the form of visual barriers, increases aggression in pig-tailed macaques, it reduces it in stump-tailed macaques (Erwin 1979; Estep and Baker 1991).

Unfortunately, we know very little about the housing and husbandry needs of many of the species that are held in zoos, which means that very often past experience (gained through personal knowledge or from zoo colleagues) or knowledge is generalized between similar species in order to create housing and husbandry regimes that it is hoped will meet the animals' basic needs. Because of this, it is important that adequate monitoring of the animals and, in due course, detailed research are undertaken so that a body of knowledge is built up to give us a greater understanding of different species' specific needs. No matter what species we are considering, however, there are various common factors, to which we can refer collectively as 'individual differences', that will affect their needs.

Individual differences are those characteristics that set one animal (individual) apart from another and affect how that animal functions within its environment. These differences include such characteristics as the animal's age, sex, reproductive status, size, and social rank, as well as its temperament (see **Box 4.2** for more about temperament or personality), health (for example, the animal's disease load), past experience, and other factors that contribute to its individuality. These characteristics place biological demands on the animal and thus affect its needs, so they have to be factored into housing and husbandry provision in the zoo. It should also be remembered that many of these characteristics will change during the animal's lifetime. Here, we will look further at how some of these characteristics affect animals' needs, and how housing and husbandry regimes should be developed to accommodate them.

Age

In many ways, the needs of old and young animals are similar, because both may have difficulty coping adequately with stressors, but for very different reasons. Old animals undergo senescence and young animals have not yet fully developed, so both groups should be considered vulnerable. Animals that are unable to cope with stressors can have compromised welfare due to an increased risk of disease and other associated deleterious consequences (this issue is explored fully in **Chapter 7**).

The period of senescence is also associated with increased **mortality** and reduced **fecundity**.
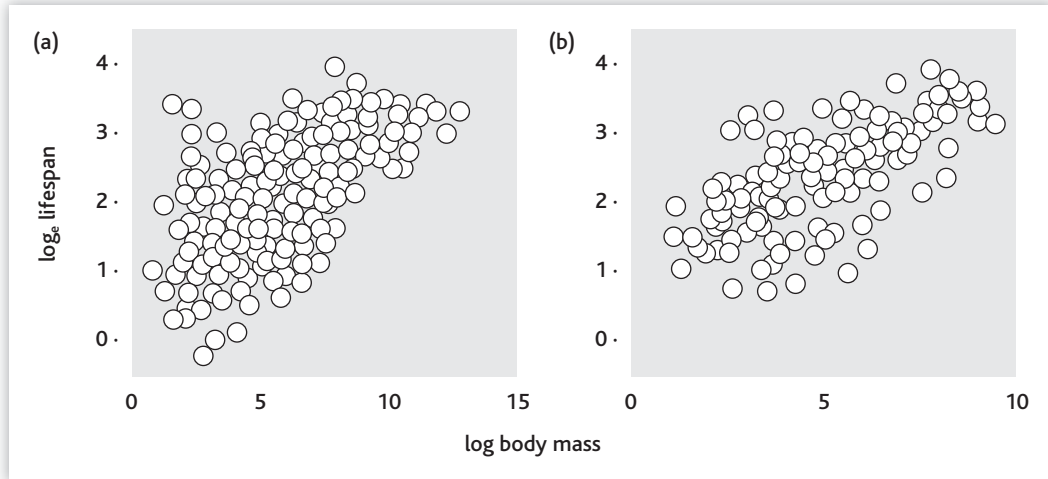
Figure 6.1 Size does matter! Speakman (2005) found that there was a significant positive correlation between an animal's size (body mass) and how long it lived. This is true for (a) mammals (N = 639) and (b) birds (N = 381). (From Speakman 2005)

Studies of ageing have shown that old animals are also associated with a higher incidence of hypothermia and hyperthermia because they are less able to thermoregulate their temperatures physically and behaviourally owing to changes in body composition and endocrine function. For example, aged mouse lemurs *Microcebus murinus* were observed to seek out warmer ambient temperatures within their enclosure and thus were shown to thermoregulate behaviourally to compensate for reduced autonomic thermoregulation (Aujard *et al.* 2006). Old animals may also suffer from sarcopenia[1] (Colman *et al.* 2005).

The sorts of histological change that can be seen in ageing human brains can also be found in brains of other mammalian species, suggesting that the process of ageing is similar in humans and other animals (Dayan 1971). Consequently, we might expect cognitive function, including memory and **learning**, to decline in older animals. Studies on ageing in mouse lemurs (e.g. Picq 2007) and rhesus macaques *Macaca mulatta* (e.g. Moore *et al.* 2006), which are both commonly used species for research on ageing, suggest that this is the case.

[1] Sarcopenia is a decline in skeletal muscle mass and function that is visible as frailty, physical weakness, and increasing disability.

Young animals are also vulnerable to stressors, just as old animals are, because they too are underdeveloped both physically and behaviourally, although in some species the effects of these can be mitigated to some extent by parental care.

Size and social rank

Larger birds and mammals live longer and require more energy to survive than those that are small (**Fig. 6.1**). This is probably because larger animals have a proportionately slower metabolism relative to smaller animals—in other words, as an animal gets larger, it requires more energy, but its rate of metabolism declines and thus it is able to use that energy more efficiently (Schmidt-Nielsen 1997; Speakman 2005) (see **section 12.2.1**). It should be noted that there are exceptions to this pattern (Speakman 2005). Large animals have a low body surface area to volume ratio, and so gain and lose heat slowly, whereas small animals have a higher body surface area to volume ratio, and therefore gain and lose heat more quickly (Schmidt-Nielsen 1997). Because of these relationships, an animal's size can tell us something about its **longevity**, its **nutritional requirements**, and the extent to which we need to provide facilities for themoregulation, such as heat lamps (see **section 6.2.3**). An animal's size, to a certain extent, also determines the

amount of space that it requires, and this is discussed in more detail in **section 6.3.3** and also in **Box 6.1**.

Within a species, larger animals are more likely to attain positions of high social dominance rank and therefore enjoy priority access to resources. This can have direct implications for many aspects of captive management, such as food presentation (see **section 12.7**). It also has implications for breeding success and social stress, because of behavioural and physiological differences between dominant and subordinate animals. These can be the result of mechanisms that are highly variable and complex, which we need to be aware of when managing social groups in captivity.

A good example of this is the African hunting dog *Lycaon pictus*. The majority of cubs in a pack of these dogs are born to the dominant male and female, both of which show significantly different hormone profiles to other animals in the pack (Creel *et al.* 1997). Subordinate females have elevated levels of oestrogen compared with dominant animals and this effectively reduces their ability to conceive. On the other hand, subordinate males have lower levels of testosterone than dominant animals, and consequently copulate at lower levels and are less aggressive. This pattern of reduced reproductive success in submissive animals is seen in some other species as well, and it has been suggested that, in primates at least, it results from social stress (Silk 1989). In the hunting dogs, however, it is the dominant animals that have elevated levels of **cortisol** compared with the submissive animals (Creel *et al.* 1997).

Previous experience

> Somehow a fuzzy, stumbling tiger kitten becomes a monstrously efficient killer. Somehow a big-footed fool of a raven fledgling becomes an aerial acrobat … How do baby animals become competent animals? While part of the answer is that cubs and kittens and chicks mature and come into their powers, another part is that they learn what they can do and how to do it.
>
> (McCarthy 2005)

Previous experience is a term used to describe the sum of what an animal has learnt during its development up to the current day. Early experiences for many species are considered incredibly important and they contribute towards an animal's survival success (see **Box 9.6**).

We have already looked at how animals learn and have pointed out how they may learn to associate with different events in the zoo (see **section 4.1.2**). For example, animals may learn to associate keepers with the provision of food, or the presence of vets with being caught or a painful incident. Therefore an animal's previous experience in captivity will affect how it perceives and responds to housing and husbandry. How, for example, will the animal respond to novelty: will it be scared or will it be curious? There is some evidence that animals which are exposed to high degrees of environmental complexity (such as **environmental enrichment**) are more able to adapt to novelty (see **section 8.6.2**). Keeping detailed records of an animal's previous experiences, including rearing, social groupings, and other aspects of housing and husbandry, will provide a fundamental insight into its behaviour and requirements in captivity.

External environmental factors

Variations in environmental factors such as climate and day length also make demands on an animal's biology and influence its needs in captivity. Many species have evolved seasonal behavioural patterns to reflect changes in resources and climate (Oates 1989; Menzel 1991). Tropical and temperate climate zones are characterized by different events, such as heavier rainfall in the tropics and shorter day lengths relative to temperate zones. Because of this, seasonal changes experienced by wild and captive **conspecifics** are frequently different, because captive exotics may live in zoos with dissimilar climates and seasons to those in which they have evolved to live. In addition, some housing and husbandry regimes may change seasonally. For example, in the UK, we experience shorter days in winter, which means that

many captive animals are fed earlier and potentially locked into sheltered enclosures for longer periods of time.

Summary of animal needs

It is likely that, within a captive group of social animals, a housing and husbandry regime will need to accommodate both the species-specific and the individual needs of the animals in the group. Therefore a good housing and husbandry regime needs to ensure that the five freedoms are met for the group, meeting any species-specific requirements, but must also retain some flexibility, so that the needs of individuals can also be accommodated. This can only be achieved through an understanding of the animal's biology and how it is affected by its captive environment, as well as regular monitoring by knowledgeable staff.

6.1.2 Keepers' needs

The fundamental role of keepers[2] is to ensure that the animals in their care have good welfare. At its most basic, keepers are responsible for monitoring the animals in their care, providing them with food and water, and ensuring that their environment is safe, clean, and enriching. Keepers are also involved in less routine activities which involve close contact with animals: for example, catching and restraining animals, introducing animals to a group, training, administering medical treatments, and many other things. Increasingly, keepers are also involved in educating the public about the animals they work with, through casual or formal conversations with the zoo visitors, and even through media performances (**Fig. 6.2**).

Keepers are part of a team of zoo professionals who work together to ensure that husbandry procedures are well informed by past experience and also by advances in scientific knowledge. Many of these husbandry procedures are described later in this chapter (see **section 6.3**) and in other chapters

Figure 6.2 As many zoos become the focus of television shows, keepers and other zoo professionals have had to include media skills in the broad array of duties that they may be required to fulfil in a day. (Photograph: Paignton Zoo Environmental Park)

within this book (see **Chapter 8** on 'Environmental enrichment', **Chapter 9** on 'Small population management', and **Chapter 12** on 'Feeding and nutrition'). This section will consider what the keepers' needs are and what measures need to be considered that might facilitate their work. It should be remembered that the steps taken to facilitate the keepers' efforts should, in turn, promote the welfare of the animals in their care.

It's all about serviceability

Small details in enclosure design and/or management practice can either facilitate or hinder the efficiency of daily animal husbandry. For example, if drains are placed at the bottom of a slope, enclosure water will run into them, but if they are placed anywhere else, water must be moved towards them, and this requires time and effort that might have been expended elsewhere. There are many such 'little' considerations that can be made to housing and husbandry that greatly facilitate the keepers, and other zoo professionals, in achieving their daily duties.

---

[2] Those charged with the daily responsibility of caring for zoo animals are frequently termed 'zookeepers' or 'caregivers', but for the purposes of this chapter we will refer to them simply as 'keepers'.

From the keepers' perspective, some of the most important and influential details that will facilitate husbandry are as follows.

- *Easy-to-clean exhibits* These can be created by providing deep-litter flooring systems, self-cleaning paddocks, the correct type of door (for example, hinged, sliding, or guillotine), correctly placed drains, and so on.

- *Consideration of how staff can move animals safely within the enclosure* It is vital that keepers can view animals easily wherever the animals are in the enclosure, especially when they are moving the animals or catching them up. There should not be any blind spots in which animals can hide from the keepers' view. This can be achieved through features such as good lighting, thoughtful design, viewing windows, and careful consideration in the positioning of enclosure furniture.

- *Providing easy access into enclosures for staff and, where necessary, vehicles* Practical considerations about how keepers and other staff service enclosures should be considered: Can all areas of the enclosure be accessed safely? Can large items be moved into and out of the enclosure? Could a keeper escape if necessary? Might enrichment be securely added to the enclosure?

How husbandry can be facilitated through enclosure design is considered in more detail in **section 6.2**, but it is important to realize that this can only be accomplished by integrating all staff that will use the facility into the design team (Coe 1999) (**section 6.1.5**).

Thinking about how the enclosure is going to be serviced, and ensuring that these activities are facilitated, helps to increase the time available to zoo professionals to perform other duties. For example, extra keeper time can be devoted to the provision of additional enrichment, husbandry training, or observing their animals.

Staff training

Trained staff are considered beneficial in all types of business, and this is supported and promoted by organizations such as Investors in People (**Fig. 6.3**). In zoos, the role of staff is varied and they are required to have many different skills, from the catering manager to the conservation officer, and the horticulturist to the head keeper. Different countries, states, or federations have legislation and guidelines to inform safe operating procedures. *Managing Health and Safety in Zoos* (MHSZ) is a document produced by the UK Health and Safety Executive (HSE). Both the MHSZ (HSE 2006) and the Secretary of State's Standards of Modern Zoo Practice (SSSMZP) (Defra 2012a) highlight the importance of training staff, and there are different government initiatives to encourage and promote this. Because this book focuses on animal management, we will look only at those zoo employees who work with the animals.

Figure 6.3 Well-trained knowledgeable staff are fundamental to achieving the mission of the zoo. In some cases this might require learning about new species, especially those whose captive management can be quite demanding such as proboscis monkeys *Nasalis larvatus* which, as browsers, have proved difficult to maintain in captivity. Recently a group moved from Singapore Zoo, who have had great success with them, to the Netherlands. (Photograph: Tjerk ter Meulen, Apenheul Primate Park)

As modern zoos have evolved, so has the role of the keepers, in terms of their expectations of the job, and the expectations of zoo employers in terms of the keepers' qualifications and experience. All zoo associations offer training opportunities; the AZA provides an extensive variety of professional development courses on subjects ranging from 'amphibian management school' to 'managing animal training and enrichment programmes', and similar programmes are offered through the EAZA Training Institute. In some circumstances zoos may host universities, colleges, or institutes, or work in close collaboration with them; for example, in the Netherlands, the research department of Artis Zoo is also part of University of Amsterdam. Alternatively, some zoos have their own academic centre (e.g. Taronga training institute, Australia), and some colleges have their own zoos for training students (e.g. Moorpark College, California). There has also been a proliferation of courses offered that include material relevant to captive housing and husbandry of exotics (see **Further reading**). Therefore it is probably unsurprising that, with the increasing competition to become a keeper, many keepers are now required to hold higher qualifications than previously was the case, and to have extensive experience of working with and around animals. For zoo professionals who do not have the resources to gain such

further professional development, for example in developing countries or poorer zoos, capacity-building initiatives have proved to be extremely effective (Melfi and Hosey 2012).

6.1.3 Visitors' needs

To meet the needs of zoo visitors, we really need to know what their motivation is for visiting zoos. It is estimated that over 700 million people worldwide visit zoos (Gusset and Dick 2011) (**Fig. 6.4**), but surprisingly few studies have been undertaken to investigate who they are (**demographics**) and why they visit zoos (motivation), or even whether they are satisfied with their visit (see **Chapter 15**). Most of the studies that have been undertaken have been completed by sociologists and environmental psychologists, and suggest that the characteristics of zoo visitors include groups, rather than single visitors, and all ages, although children usually predominate and families are the most frequent type of group (Cheek 1976; Morgan and Hodgkinson 1999; Turley 1999).

We will look in more detail at what people do when they are at the zoo in **Chapter 13** on 'Humans in Zoos', but here it is worthwhile considering briefly some studies on what motivates people to go to the zoo, because this can then help us to understand their needs.

Figure 6.4 As discussed in **Chapter 13** on 'People in zoos', there are many contexts in which visitors share the world of zoo animals, even those who live in a completely different environment. Underwater viewing has enabled people to see aquatic animals better, but also allows the animals to see the visitors, as here at Nagoya Aquarium where a Pacific white-sided dolphin *Lagenorhynchus obliquidens* takes an interest in a zoo visitor (Photograph: Jereon Stevens, Nagoya Aquarium).

An early study by Kellert (1979) found that the underlying motivation of zoo visitors in the USA was to educate their children (36 per cent), to have a fun day out with family and friends (26 per cent), to see animals (25 per cent), and to be around wildlife (11 per cent). Wilson (1984) has suggested that people are inherently biophilic;[3] they like nature and want to be around it.

This is a perspective which matches that held by many zoo professionals, who believe that the zoo can provide visitors with much more than just physical access to animals, plants, and (usually) green spaces; they allow people to experience these things with all of their senses, not just to view them as they would a television documentary (see **Foreword**). Thus, we can regard zoos as offering an opportunity for ecotourism or a 'taster of the wild' (Mason 2000). Implicit in the term 'ecotourism' is that a triple bottom line is achieved: Townsend (2009) outlines how zoos and aquariums can work to support ecological integrity, contribute to society, and also maintain economic growth. It is also important that zoos provide these 'wild' opportunities as a convenient, safe, and comfortable day out (Beardsworth and Bryman 2001). Morgan and Hodgkinson (1999) have cautioned that studies of zoo visitor demographics and motivation should not necessarily be generalized across zoos, because many factors affect people's decisions to visit a zoo, including its location, what animals it holds, and probably other factors as well. A recent study by Whitworth (2012) supports this, suggesting that type and number of species was a better determinant of zoo popularity than other factors, like the demography of visitors. Nevertheless, there does seem to be a consistency in people's motivation to visit zoos. For example, Andereck and Caldwell (1994) found that education and recreation constituted the main reasons why people visited the North Carolina Zoological Park, which is consistent with Kellert's (1979) results. Similarly, the motivation behind visits to UK zoos was investigated by Turley (1999), who found it principally to be

recreational, rather than for an educational experience or to support conservation. Indeed, Turley (1999) concluded that most zoo visitors wanted to see and enjoy animals, unlike visitors to museums, who wanted to understand; thus, zoo visitors want '*entertaining, compelling and effectively staged*' events (Beardsworth and Bryman 2001). There is, then, a need to incorporate educational opportunities into what most zoo visitors consider to be a 'fun day out' (Brodey 1981). This helps us to understand the statement by the Director Emeritus of the Columbus Zoological Garden, who said that he would rather '*entertain and hope people learn than teach and hope people are entertained*' (Hanna 1996). This then facilitates the communication of the conservation message, as Baba Dioum (an environmentalist from Senegal) is quoted to say '*in the end, we will conserve only what we love, we will love only what we understand, we will understand only what we are taught*', although, in a recent meeting, it was suggested this premise be turned on its head—that in fact '*first people need to love, then they will learn and then they will act*' (Dickie 2012, personal communication).

If zoo visitors principally want to be entertained and to have a 'good day out', then there are some basic requirements that they will expect, including the provision of amenities and, above all, good service. If these requirements are not met, the entertainment and educational value of the zoo experience can be undermined:

> The young woman who waited on us [at the snack stand] was so uninterested and the food was so poor that my students talked of nothing else the whole afternoon. The magical opportunity created by the $15 million exhibit investment was quenched by the most junior employee in the whole park!
>
> (Coe 1996)

But it is the animals that the visitors have come to see. Bitgood *et al.* (1988) considered that a visitor's ideal exhibit was a **naturalistic enclosure**

---

[3] Biophilia is the concept that people have a love of nature and natural things. It has been promoted by Edward Wilson and Stephen Kellert as the idea that people need contact with nature.

holding a large active mammal, preferably with young. This seems a rather simplistic view, but subsequent research has supported it. Visitors perceive animals in traditional enclosures with bars as having compromised welfare compared with those in greener enclosures (Turley 1999; Melfi *et al.* 2004b).[4] Visitors also spend longer observing **free-ranging** tamarins, which are more active than their counterparts in 'traditional' cages (Price *et al.* 1994), and visitors at the Zurich Zoo spend more time observing larger animals (Ward *et al.* 1998) (**Fig. 6.5**—but also see **section 13.1.2** for an alternative explanation).

Zoos can provide visitors with a magical experience. Vining (2003) describes how interactions with animals can be magical and thus create lasting impressions, which might include medically therapeutic effects, or might encourage an attitude that cares for animals. Fiedeldey (1994) noted that, in the right circumstances, even the tracks of an animal that you do not actually see can be exciting. Close experiences with an animal are particularly rewarding. In many zoos, there have always been opportunities to get close to some species: for example, in the **petting zoo** or in animal-handling sessions. Cheyenne Mountain Zoo has gone a step further, and has built into its zoo animal management and visitor experience philosophy the concept of providing visitors with a 'defining moment' (Chastain 2005). It provides some visitors with a unique opportunity for close contact, which is not usually possible on a zoo visit. This might entail getting close to a giraffe or helping the keeper to scatter food around an enclosure before the animals are let out.

The demand for these 'close encounter' experiences is so high that schemes exist under which visitors can pay to feed animals or even to be a 'keeper for the day', for example, at Taronga Zoo, Sydney, Australia (**Plate 13.1**), and Paignton Zoo Environmental Park, UK (Martin and Melfi 2013). In these situations, animals in zoos are no longer only to be viewed by visitors, but they are
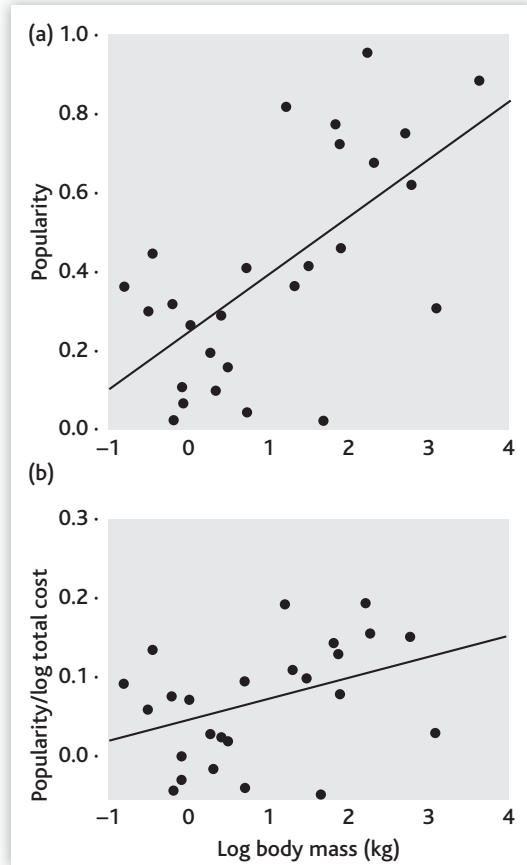
Figure 6.5 It is probably unsurprising that larger animals are perceived by many zoo visitors as the more interesting. (a) Here, you can see that there is a positive correlation between popularity, as rated by zoo visitors, and zoo animal size. (b) It is interesting to note that there is also a positive correlation between the cost of maintaining animals and their overall size (Ward *et al.* 1998). Issues of animal size in relation to their attractiveness to visitors and their inclusion in zoos are discussed further in **section 13.1.2**. (From Ward *et al.* 1998)

expected to perform and/or interact with visitors. It is not in doubt that this provides a more compelling educational message, but it is debated exactly what that education message might be (Beardsworth and Bryman 2001). Much of this discussion is based on speculation, because few **empirical studies** have been undertaken to explore zoo visitors' attitudes to animals and, more

---

[4] Interestingly, however, Verderber *et al.* (1988) found that elderly visitors to zoos were anxious when

animals were not presented behind bars and had 'invisible' barriers.

importantly, how 'interactive' sessions may influence these. Robinson (1989) has suggested that the beneficial 'message' gained from seeing animals in zoos can be lost when the animals are taken out of context, away from their naturalistic environment and into a show arena (Robinson 1989). However, this can be mitigated by providing a live-animal demonstration within the animal enclosures. At Zoo Atlanta, for example, husbandry training of the otters was incorporated into the visitor experience (Anderson *et al.* 2002). Visitors were observed to stay at the exhibit longer, and had more positive attitudes towards the animals and the zoo in general, when they observed husbandry training of the otters.

The topic of visitor education and awareness raising is one to which we will return in **Chapter 13**; some of these issues are also explored in **Chapter 15**.

6.1.4 Other interested parties

We have considered how the needs of animals, keepers, and the visiting public have implications for housing and husbandry procedures, but there are other factors that can impact on these as well.

Reducing environmental impact and promoting sustainability

We are all very aware now that many of our natural resources are diminishing and that there is a need to consider the impact on the environment of the way in which we live our lives; the same philosophy applies to how businesses should operate. Many zoos work hard to convey the message that conservation of our precious resources is necessary, and the first step that they can take is to 'put their words into actions' by applying those principles to the way in which they operate the zoo.

There are many ways in which zoos can be 'environmentally friendly'. Just like other businesses, they can implement environmentally sound work practices to minimize their impact on the environment. For most zoos, like other businesses, this requires setting up an environmental management system, which 'identifies, measures,

and reduces the organization's impacts on the environment' (Turner 2009). An internationally recognized certificate, ISO 14001,[5] is awarded to those businesses that are able to demonstrate that they implement these methods of best practice. In 2006, two BIAZA member zoos were awarded ISO 14001, and in 2006 this rose to a further five BIAZA member zoos (Stevenson 2008). A further 55 per cent of BIAZA zoos had environmental policies in 2006 and BIAZA produced documentation to facilitate further the work of their member zoos towards **sustainability** (Stevenson 2008).

The following are some examples of the many opportunities available to zoos to enable them to operate 'environmentally':

- the sourcing, efficient use, and disposal of resources should be executed in a such a way that it minimizes the zoo's environmental impact, for example, by using sustainable energy and products, such as solar power, reclaimed water, and Forest Stewardship Certificate (FSC) approved wood;

- ensuring that these resources are used wisely (by turning off power when it is not needed, minimizing packaging on products bought and sold, recycling products, and so on);

- where possible, purchasing products locally or as part of fair trade or **organic** schemes to ensure that the environment is not harmed elsewhere.

The issue of sustainability is discussed further in **Chapter 15**.

Plants: pretty, food, poisonous, or a natural barrier?

Although this is a book about zoo animals, plants must be mentioned because they play a huge role in animal housing and husbandry, from the exhibition to the maintenance of zoo animals (see review by Frediani 2009). Plants are fundamental in the creation of 'naturalistic' enclosures, which are now very common in zoos and popular with the

---

[5] A reminder that ISO refers to the International Standards Organization.

visitors (Jackson 1996) (**section 6.2.1**). They can provide natural complexity within the enclosure, providing locomotion and play opportunities, as well as shelter from the elements. If the right plant species are chosen—normally those that are sympatric with the exhibited animals' wild conspecifics—they can provide an ecologically relevant landscape for the animals being exhibited, which serves to facilitate visitor education programmes and the creation of bioexhibits. Unfortunately, this might mean that, in their native habitat, the plants chosen for the exhibit would be a food source and thus vulnerable to being eaten.

When planning which plant species are going to be used in animal exhibits, their function should be identified from the outset. The big question is: does it matter if the animals eat them? To any botanist, the answer is surely 'yes', but in some situations, plants are provided specifically to enable the animals to feed and forage within their enclosure. It could be argued that, unless plants are protected, they are all potential food items. As such, the plants chosen need to be non-hazardous and non-toxic. The differentiation is necessary because some plants may cause injury from thorns and other physical defences, while others may cause illness because they contain distasteful or toxic chemicals (see **Box 12.1**). Plant lists that provide information on plant toxicity are available, and these should always be consulted before selecting plants for exhibition. There are various different 'plant lists' compiled by national and regional zoo associations (e.g. BIAZA plant database (Plowman and Turner 2006)) or by keeper associations (e.g. the Dutch Zoo Keepers Association produced a browse book with an identification guide). There are quite a few examples of plants being provided solely to feed animals on exhibit, with grazing animals (both birds and mammals) being the most obvious. In these situations, it is necessary to have some idea of nutritional value and the extent to which the animals consume the plants within their enclosure (we will return to this issue in **Chapter 12** on 'Feeding and nutrition').

If we do not want the plants to be eaten, because they are endangered, toxic, or serve some other function, there are various ways in which they can be protected: they can be kept behind barriers, for example, in much the same way as barriers keep animals and visitors separated (Frediani 2009). Electric fencing is the most frequently used barrier to protect plants from animals, although physical barriers are also used. For example, large trees that provide shelter, in the form of their canopy, can be protected with barriers at their base or halfway up the tree to prevent animals from climbing them. In other circumstances, plants can themselves be used as barriers, especially if they have the defences that we mentioned above (such as thorns or distasteful chemicals). Plants' physical defences, such as thorns, can be enough to discourage both animals and zoo visitors alike from going near them for fear that they might be stung or injured.

Giving researchers somewhere to hide

Because research is now a key goal of zoos (see **Chapter 14**), the needs of researchers are increasingly being integrated into zoo enclosure design. Some zoo exhibits now include areas from which researchers can gain unobstructed views of their research subjects—the animals. This has been achieved through features such as the provision of elevated observation areas, additional 'researcher only' windows, and closed-circuit television (CCTV) cameras. At the Lincoln Park Regenstein Centre in Chicago, IL, for example, special windows constructed of three triangular panes protrude into the ape exhibit to give researchers an all-round view. Panda Cam at San Diego Zoo in California, provides live video footage of the pandas to researchers and visitors, and also on the Internet.

Research into the anatomy and locomotion of animals can also be facilitated through enclosure design. For example, at Dierenpark Planckendael, in Belgium, the study of terrestrial bipedal locomotion in bonobos *Pan paniscus* has been achieved by incorporating force plates into a walkway that the animals use to gain access into and out of a play room (D'Aout *et al.* 2001). This walkway is surveyed by CCTV cameras and has a backdrop that provides scale (**Fig. 6.6**).
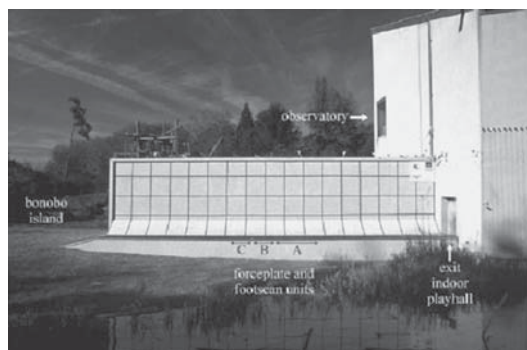
Figure 6.6 Conducting zoo animal research is clearly facilitated at some exhibits, where the needs of researchers have been integrated into the enclosure design. Here, we can see a walkway, which is the main route that bonobos *Pan paniscus* take between their inside and outside enclosure areas, constructed at Planckendael, Belgium. This simple addition has enabled researchers to learn a great deal about locomotion in this species (e.g. D'Aout *et al.* 2001). (Photograph: *Folia Primatologica*)

Building regulations: what can be practically accommodated?

It is necessary to consider all the stakeholders (including those previously mentioned in this section), but among the most important of these when designing exhibits are the builders. The design of zoo enclosures has to satisfy all the same building regulations that are necessary for 'ordinary' buildings, including environmental and energy-saving considerations. In the UK, building regulations include everything from ensuring disability access to providing sufficient drainage, and are concerned with whether the physical demands on the exhibits can be met: Is the building strong enough to keep in elephants, for example? Will the mesh roof withstand snow? How will 500,000 visitors negotiate their way around the exhibit? Is the glass really shatterproof?

Of utmost importance is that the finished exhibit, and its surrounding area, will be safe for zoo animals, staff, and visitors alike.

Health and safety considerations

The health and safety of keepers—and, indeed, of all zoo professionals—while at work is of the utmost importance. The UK Health and Safety Executive (HSE) has produced a summary document detailing the necessary steps that should be considered and measures that should be employed by zoo operators to ensure safe working conditions for their employees and those who enter the zoo, such as visitors, contractors, and volunteers (HSE 2006). Much like the SSSMZP (Defra 2012a), this document, *Managing Health and Safety in Zoos* (MHSZ), outlines the measures that zoos should take to adhere to the relevant legislation, particularly the Health and Safety at Work etc. Act 1974 (see **Table 3.2**). The inspection of zoos for compliance with health and safety regulations occurs in addition to the zoo licensing inspection. (See **Chapter 3** for more on zoo licensing.)

There are three main sections to MHSZ: safety issues, health issues, and emergency procedure. Much of the document refers to issues that are common to all businesses (for example, 'slip and trip' hazards, noise at work, and emergency procedures if there is a fire), or are common to work with animals (for example, safety issues related to veterinary procedures, safe animal handling, and public contact with animals), but it also includes some areas that are unique to zoos (safety in large drive-through paddocks and animal escape procedures). For example, this document outlines some recommended precautions that should be taken to reduce the risk of animal escapes:

- nominating a person and deputy to take charge of the situation and make any important decisions;
- raising the alarm and reporting incidents to appropriate personnel as quickly as possible;
- communications with entrances/exits and allocating responsibilities for closure where necessary;
- arrangements for the evacuation or safe confinement of people in the zoo, ensuring that those situated away from buildings receive appropriate assistance as quickly as possible;
- managing crowds safely in an emergency situation and the giving of directions;

- a strategy for recapture appropriate to the various types of animal kept;

- liaison arrangements with senior zoo personnel, vets, etc. for the recapture plan, which should include the use of radios, equipment, vehicles, firearms;

- identifying essential employees etc;

- briefing staff as to their roles and responsibilities during a recapture operation including the recapture of animals escaped beyond the perimeter of the zoo;

- arrangements to locate the escaped animal;

- arrangements to keep the animal under observation while recapture plans are being formulated, and the movement of key personnel to the area once the escaped animal has been located;

- the provision and location of the necessary capture equipment, e.g. nets and firearms/darting equipment. Torches will be invaluable for night escapes and should be located in a designated area;

- alerting external emergency services, e.g. police, where necessary;

- stand-down arrangements on the completion of the recapture operation, including notifying all relevant personnel and external organisations involved.

(HSE 2006)

Like all businesses, zoos should have written health and safety policies. They should also assess the risk to staff, volunteers, and visitors to the zoos that may be incurred by the activities of the zoo in general; this forms the basis of the risk assessment.[6] All identified risks should be considered and appropriate measures put in place to ensure that these risks are minimized to a safe level. It is also noted that staff should be capable, through

having had sufficient experience and/or training, to carry out the work that is expected of them.

Health and safety issues are also dealt with in the SSSMZP (Defra 2012a): Section 8 is all about visitor health and safety at the zoo.

6.1.5 Incorporating all needs into housing and husbandry

Good zoo housing and husbandry ensures that the needs of all stakeholders are considered, and that, where there is conflict, resolution is sought and agreement achieved on a final decision. A multidisciplinary team is important for this because:

(1) many zoo mission statements imply values and goals that affect a variety of people (see **section 2.5.1**);

(2) it will ensure that the diverse skills and views of all zoo staff are considered, which will subsequently result in fewer oversights and more people will feel involved, responsible, and thus supportive of the development across all zoo departments;

(3) there are many benefits associated with working in a multidisciplinary team, not least learning what colleagues do and their point of view;

(4) innovative ideas usually occur during discussions between professionals with different backgrounds and viewpoints (Coe 1999).

Nevertheless, some conflicts of interest do occur. The following are some examples of the sorts of situations in which such conflicts might happen:

(1) visitors want to be able to view the animals easily, whereas the animals want to be able to hide;

(2) visitors want animals to have large complex enclosures, whereas keepers need to be able to service the enclosures;

(3) plants provide a good-looking enclosure, but the animals may want to eat them.

[6] A useful guide to carrying out a risk assessement in a zoo setting can be found in the *Zoos Expert Committee Handbook* (Defra 2012b).

How might we resolve conflicts of interest such as these through good housing and husbandry? In relation to the above, possible resolutions are:

(1) visitor viewing can be restricted by various methods, including camouflage netting, which still affords visitors a view of the animals, but allows the animals to feel relatively hidden (Blaney and Wells 2004) (**Fig 13.14**);

(2) when paddocks or inside enclosure areas are large enough, they can, in a sense, become self-cleaning, because voided faeces represent such a low presence that they rot away into soil or deep litter bedding (e.g. Chamove *et al.* 1982);

(3) plant species can be selected that are non-toxic, but unpalatable, or which protect themselves with thorns and which animals tend not to eat (Wehnelt *et al.* 2006).

These and other examples will be expanded upon in **section 6.2**.

This leaves only the problem of what happens when a compromise does not present itself, leaving the conflict difficult to resolve. In this case, it seems intuitively right that an emphasis on the animals' needs should be prioritized, because the zoo's primary goal is to conserve species and meet their welfare needs. In recent years, however, there has been a dramatic change in the balance from prioritizing animals' needs to meeting the needs of visitors (**Fig. 6.7**). But does it cause problems if the needs of the zoo visitors shape enclosure design and, ultimately, housing and husbandry in general? Visitors consistently want to see naturalistic enclosures and active animals (playing, climbing, and eating), factors that they also believe represent good animal welfare (Melfi *et al.* 2004a). The aesthetics of an enclosure, the level of activity displayed, and the appearance of an animal, not whether it has enrichment in its enclosure, are used by visitors as indicators of animal well-being (McPhee *et al.* 1998).

However, we should remember that zoo visitors are not trained to understand the complexities of assessing animal welfare. It is also unclear whether they genuinely consider, from an objective standpoint, what housing and husbandry factors promote good welfare, or whether their opinions are shaped to fit what they would most like to see. So shaping zoo enclosures purely to meet the needs
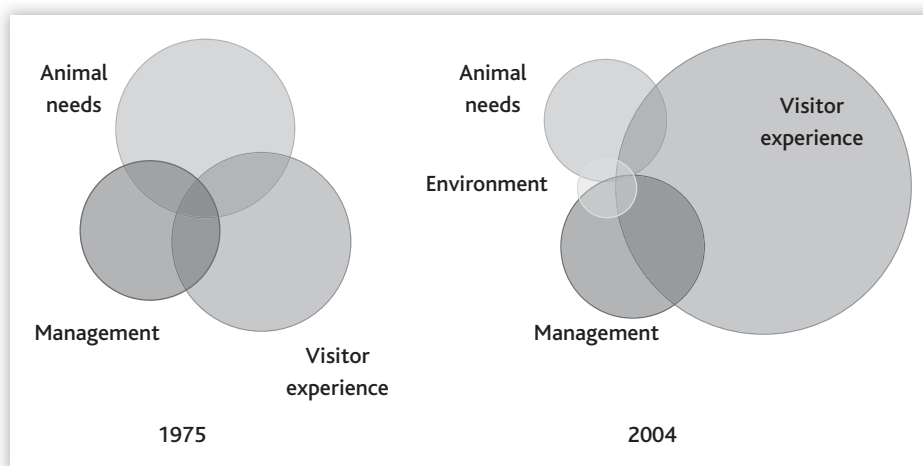
Figure 6.7 There are three main stakeholders whose needs should be borne in mind when designing animal exhibits: the zoo animals themselves, the zoo professionals (notably the keepers), and the visiting public. Melfi *et al.* (2007) suggested that the emphasis placed upon each of these stakeholders has changed over time, which was portrayed by the approximate proportion of content focusing on various elements of design, gathered from the *Proceedings of the First Zoo Design Symposium* (1975) and estimated from abstracts of the *Sixth Zoo Design Symposium* (2004). Notably, emphasis of the animal's needs has reduced, while attention to the visitor experience has risen. However, it is heartening to see that the inclusion of the fourth stakeholder, the environment, seems to be emerging. (Picture: Whitley Wildlife Conservation Trust)

of visitors is potentially perilous for the animals' needs, but also undermines the needs that have been identified for the other parties affected by zoo animal housing and husbandry.

The bottom line in the UK, and for many other zoos worldwide, is that we rely on the admission fees paid by visitors to ensure the zoo's future and thus its activities. Because visitors know what they like, what they want, and what they expect from a zoo, it is up to zoo professionals to ensure that zoo visitors are educated about these issues so that they can make informed judgements about animal welfare, zoo enclosure design, and **exotic animal** behaviour. If this can be accomplished, visitor needs will include many factors that enhance animal welfare, and this will provide overlap between animal, keeper, and visitor needs.

6.2 Advances in enclosure design

Obvious changes have occurred in zoo enclosure design over the past few decades. These can be linked to changes in the way in which we perceive and treat animals within our society (see **section 2.3**). They also represent a greater influence of the visitors' needs being incorporated into the design process (see **section 6.1.5**). Our knowledge of animals' needs is also greater today than it has ever been, so we are more able to accommodate these within enclosure design—although we should not be complacent about this, because there is always more to learn.

6.2.1 The evolution of enclosure function

This section is not intended to be an exhaustive overview of the methods used to describe and design enclosures, but to provide an overview of those terms that are most commonly used and a balanced perspective from which to assess their merits.

Various terms are used to describe zoo enclosures: hard or soft (of architecture); first, second, or third generation; barren or complex. All these terms exist on a sliding scale. 'Barren' enclosures,

for example, are considered to be those with few, if any, objects or furnishings, but as objects and furnishings within the enclosure increase, so does its 'complexity'. Enclosure complexity, as a concept, is thought to provide the appropriate physical and psychological **stimuli** necessary to provide captive animals with the opportunity to express 'wild' behaviours (Hutchings *et al.* 1978; Ogden *et al.* 1993).

Naturalistic enclosures

It is clear that hard barren, first-generation enclosures have been making way for soft complex second- and third-generation zoo enclosures. This evolution in enclosure design has followed an intuitive path towards naturalistic enclosures—that is, aesthetically pleasing enclosures that follow the simple idiom that 'green is good'. Giving the impression of a greener enclosure requires additional planting, but also the removal of bars and other harsh-looking structures within the enclosure. Modifications can be made to 'naturalize' hard enclosures by adding complexity or natural materials (Coe 1989).

Polakowski (1987) noted that naturalistic enclosures can be designed and constructed in three different ways, which affect their functional utility for the animals and thus change the way in which they meet the animals' needs. Naturalistic enclosures could be considered:

(1) realistic, reproducing the animals' wild habitat, including land formation and plant life;

(2) modified, simulating the animals' wild habitat by using available materials to substitute for the real thing—for example, by using different vegetation and land formations present at the zoo;

(3) naturalistic, in which no attempt is made to duplicate the animals' wild habitat and natural materials are used in a stylistic way.

If we take this concept a little further, we arrive at **immersion exhibits**.

More than 30 years ago, Jones *et al.* (1976) coined the term **landscape immersion** to describe a situation in which animals and visitors would share the same setting, but not the same space. The goal of immersion was to continue landscaping

beyond the animal exhibit into the visitor area, with the aid of invisible barriers, to provide visitors with the sensation that they were 'in' the animal's habitat (Coe 1994). When exhibiting zebra, for example, '*the entire setting* [should] *look, smell, and feel as if* [the visitor has] *left the zoo and entered the African savannah*' (Coe 1985). Immersion exhibits (**Fig. 6.8**) are associated with additional theming, to ensure that educational signage, merchandising, and retail amenities do not detract from the visitor experience of, for example, 'Africa'.

Human–animal contact

The degree to which visitors and animals come into contact with one another also varies between enclosures. All the enclosures considered so far ensure that animals and visitors are separated by barriers; this is a good idea for many reasons, not least of which is the health and safety of both animals and visitors. For some species, this division has been allowed to lapse and **walk-through exhibits**, which have been in existence since the early 1920s (Olney 1975), have been developed. Recently, there has been a proliferation in the number and the diversity of species that are presented in this format (Kreger and Mench 1995).

Walk-through exhibits—and their aquatic, swim-through, cousins—still keep animals contained within a fixed boundary, but allow visitors to enter the exhibit. Unlike petting zoos, containing domestic animals, and some **touch stations** in aquariums, walk-through exhibits do not encourage 'actual' contact between visitors and animals. The separation between zoo animals and visitors is completely removed when animals are managed as free-ranging species; these animals are no longer restricted by exhibit perimeters and are more or less allowed to roam wherever they please—although the zoo does not want them to leave the zoo grounds, so appropriate barriers ensure they do not roam too far (see **section 6.2.5**).

There are obviously both advantages and disadvantages associated with these different kinds of exhibit, and these can best be understood by going back and thinking about the needs of the different stakeholders (which we explored in **section 6.1**). There is substantial empirical evidence that demonstrates

that complex enclosures meet the needs of animals far more effectively than **barren enclosures** (see **Box 6.1** and also **Chapter 8** on 'Environmental enrichment'). For example, after a group of mandrills *Mandrillus sphinx* were moved from an 'old traditional' enclosure to a 'new natural' exhibit, which was more complex, they were observed to display less stereotypical behaviour and their activity levels rose (Chang *et al.* 1999) (see **section 4.5.3** for more about this study). These changes in behaviour were considered positive, because they brought the behaviour of the captive mandrills closer to that of wild baboons.

The impact of naturalistic and immersion exhibits on the different stakeholders is a little less clear-cut. In terms of the animals' needs, naturalistic enclosures will only be beneficial if they functionally contribute directly or indirectly to the animals' lives. It probably matters little to the animal whether the additional greenery or structures are just like those of their native habitat or are simulations; what is likely to be more important to them is whether the vegetation provides much needed shade, or climbing opportunities, or supplementary food. It is always worth considering whether naturalizing the exhibit has increased or decreased enclosure complexity. A recent survey by Fàbregas *et al.* (2012) used results from zoo inspections and accreditations to compare the enclosure suitability of sixty-three Spanish zoological parks. From the data they collected, they determined that 77.8 per cent of naturalistic enclosures provided a suitable environment for the resident animals, versus 39.7 per cent of non-naturalistic enclosures. In terms of the visitors' needs, however, at least one study has shown that the aesthetics of the enclosure—principally, how much green there is—greatly affected whether visitors liked the enclosure and also appeared to affect their views about the welfare of the animals (**Fig. 6.9**).

Sometimes, naturalistic and immersion exhibits are considered restrictive by keepers. Trying to ensure that enclosures and fittings are consistent with a naturalistic theme can sometimes go against the interests of the animals, because non-natural fittings and enrichments are more abundant and often cheaper than their natural-looking

Figure 6.8 One technique employed to increase the visitor experience is to reduce the gap between them and the captive animals that they have to come to see. This can be accomplished by using different barrier types (**Fig. 6.12**), but also by making objects accessible to visitors and animals. Here is (a) a log at the Toronto Zoo, and (b) and (c) a safari jeep in Werribee Open Range Zoo, Victoria, both of which bisect the animal–visitor barrier. (Photographs: Vicky Melfi)

Box 6.1 SPACE VERSUS COMPLEXITY

Zoo visitors sometimes remark that enclosures should be bigger, but how valuable is enclosure size and how big does an enclosure need to be? Enclosure size can compromise animal welfare if it restricts behaviour, or leads to **environmental challenge** or crowding (see **Chapter 7**). It is difficult to decide empirically how big an enclosure needs to be for any one animal, and thus how much space should be allotted to a group. There is some evidence that an animal's home range or territory in the wild could predict how restricted it may be in captivity (Clubb and Mason 2007). This is supported by the generally held assumption that as enclosures become proportionally smaller, they compromise animal welfare more.

However, this type of analysis is difficult to test empirically and does not necessarily provide a guide to how big zoo enclosures should be. A more pragmatic approach is to ensure that enough space is provided to enable the expression of wild behaviours and, more importantly, those behaviours required to limit stress, such as distancing and comforting behaviours (Hediger 1955; Berkson et al. 1963). Certainly, an enclosure should be bigger than an animal's **flight distance** to ensure that the enclosure perimeter, and thus visitors or neighbouring animals, do not infringe upon it. Within the laboratory community, there has been a lot of research into optimal enclosure size (e.g. Line et al. 1989a, 1989b, 1990, 1991). Some of these studies have highlighted that additional space has not necessarily improved welfare (Woolverton et al. 1989; Crockett et al. 1993a, 1993b; Crockett et al. 1994). This suggests that cage size is unimportant, because more or less barren space was of no consequence to captive primates. However, the contents of the space (i.e. its complexity) were

important (Reinhardt et al. 1996). This conclusion is supported by many studies that demonstrate that modifications to enclosures (whether zoo, laboratory, or farm) to increase complexity, are associated with many welfare improvements, including reduced **stereotypies** (Whitney and Wickings 1987; Chamove 1989) (see **Chapter 8** on 'Environmental enrichment').

Therefore space alone may only affect captive animal welfare if it falls below a certain threshold; above that threshold, enclosure complexity may contribute more to welfare and behaviour. Indeed, there are a number of studies that show that zoo-housed animals do not fully utilize the space provided to them, but display distinct preferences for certain areas and spent much of their time in those areas (e.g. Ogden et al. 1993). In a study by Wilson (1982), enclosure complexity was identified as more important than enclosure space in the determination of gorilla *Gorilla gorilla* and orang-utan *Pongo pygmaeus* behaviour. However, when Perkins (1992) replicated this study, enclosure space and complexity were considered highly interrelated and therefore considered to affect behaviour together. This change probably represents a dramatic change in enclosure design, as part of which all enclosures are now much more complex; in older exhibits, enclosure complexity and size were more uniform.

There is a general acceptance that complex enclosures promote good welfare, which has led to the incorporation of complexity into enclosure design, and appears to have resulted in zoo enclosure size and complexity increasing in parallel (Perkins 1992). To conclude, therefore, zoo housing is considered 'good' if it is complex, dynamic, and large enough to hold appropriate social groups (Mallinson 1995; Newberry 1995).

alternatives (see **Chapter 8**). Looking at some of the newer zoo enclosures, it is possible to detect what Beardsworth and Bryman (2001) describe as the 'Disneyfication' of zoos, by which they mean essentially that an emphasis has been placed on the theming of exhibits. There are many advantages

associated with this trend, notably the enhancement of the visitor experience. But whether the expense of some themed exhibits can be justified in terms of achieving the core goals of zoos (conservation, education, and research) is an issue that will surely be debated for some time to come.
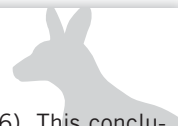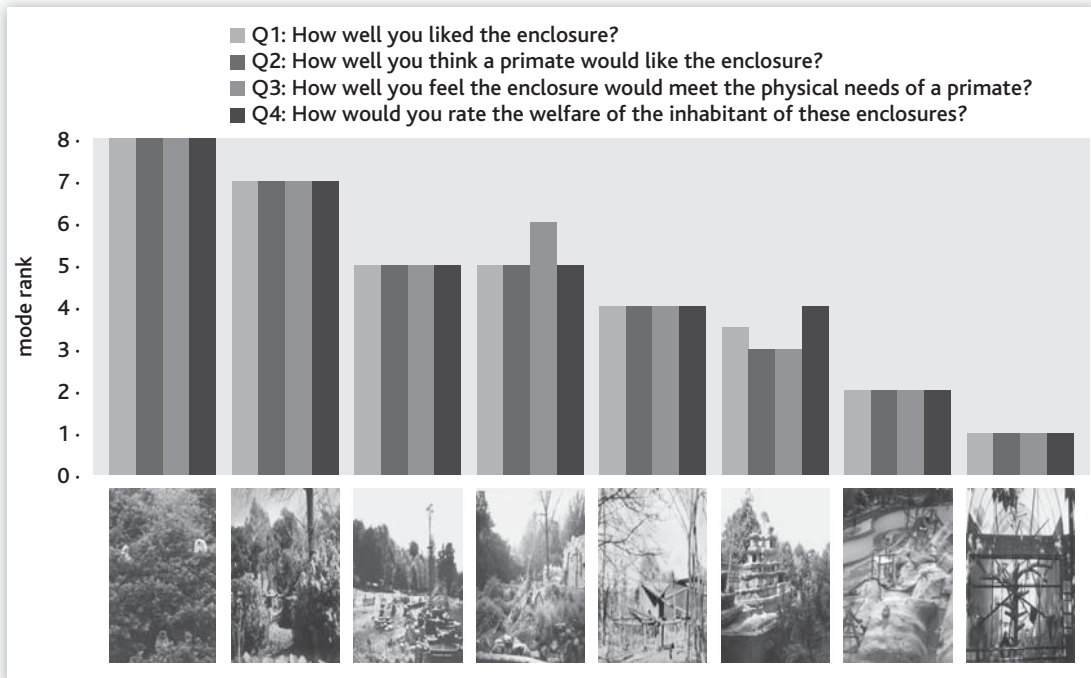
Figure 6.9 In a study of visitor perceptions at Paignton Zoo Environmental Park, UK, visitors were shown several pictures of enclosures and asked to rate them according to a series of questions. As you can see from the graph, visitors preferred enclosures that were more naturalistic, and considered that these enclosures would best meet the needs of the animals and thus promote better welfare for them. (Photographs: Vicky Melfi)

Jon Coe, who has been particularly influential in the design of zoo enclosures and especially the integration of stakeholders into the design process, has also pioneered an integrated approach towards housing and husbandry (Coe 1987, 2006). In an approach that is termed 'activity-based design', Coe (1997) suggested that the emphasis of the zoo enclosure should be to provide animals with the opportunities to express 'natural' behaviours, and keepers with the access to provide enrichment and/or husbandry training, both of which would enhance the visitor experience and increase possibilities for learning. Interestingly, he believed that all of this could be achieved because '*whether* [enclosures] *were simulations of naturally or culturally derived habitats or pure functional facilities, these environments are abundantly provided with appropriate behavioural opportunities for the animals, keepers and zoo visitors*' (Coe 1997). However, getting agreement among all stakeholders is not always easy, as illustrated in **Fig. 6.10**.

6.2.2 Basic housing

There are certain basic requirements that should be met by all animal housing, whether for exotic or domestic species. For example, conditions should be provided to ensure that the five freedoms are met (see **Chapter 7**). Standard 2 and Appendix 8 of the SSSMZP (Defra 2012a) both detail the minimum requirements that zoos should aim to achieve when housing exotic species; standard housing requirements are also thoroughly dealt with in other core texts and guidelines (for example, for domesticated species, see Wathes and Charles (1994); for laboratory-housed animals, see Poole (1999)).

In the following sections, we will consider how even basic housing requirements, such as climate control, the provision of water, and ensuring the safety of animals, need to include the exotic animals' species-specific needs. The issue of **stocking density** and how much space should be made available to animals is covered in **section 6.3.3**, and the relative importance of enclosure size versus

Figure 6.10 Views of curators and keepers might not always agree. '*We've spent half a million dollars making this zoo habitat exhibit look like a natural jungle to present a message about wild animals. You've stuffed it up with cheap playground equipment!*' exclaimed Mr Hafter B. Green, of the Exhibits department.

'*Gorillas need more than bushes,*' responds Ms Pollyanna Pett, animal keeper. '*These red boomer balls and colourful climbing cables are easily available. Besides, zoos are for the animals first … without the animals we wouldn't have a zoo!*'

'*Wrong! Zoos are for people first,*' retorts Mr Green. '*Without visitors, we wouldn't have a zoo.*' (From Coe 2006; Picture: Phil Knowling)

enclosure complexity is discussed in **Box 6.1**. Some scientific research has been undertaken to study the impact of housing and husbandry practices on zoo animal behaviour and biology (see **section 6.4**; see also Kleiman *et al.* (1996)). Unfortunately, however, owing to the diversity of species held in zoos, much of our knowledge of the impact of housing and husbandry regimes and its impact on animals comes from anecdotal information and the experience of keepers, although more objective sources of information should always be sought (for example, the SSSMZP; see **section 6.5**).

6.2.3 Climate control

The provision of a suitable climate is essential for maintaining good animal welfare and, in many species, can also affect breeding success. Furthermore, appropriate climate control is central to the management of disease. For example, Exner and Unshelm (1997) demonstrated that variations in airborne micro-organism concentrations, recorded over a year in exotic felid enclosures, were affected by climatic conditions.

An animal's preference for resources within its enclosure will vary over the day, or season, so it is good practice to provide animals with variations in climate and other factors within their enclosure. Unfortunately, few studies have been carried out to study the combined impact of these climatic variables on zoo animal behaviour or welfare. An exception is a study by Young *et al.* (2012) which documents the impact of changes in microclimate, air temperature, relative humidity, solar radiation, and wind on the behaviour of African lions and Amur tigers. Though based on a small sample size, this study provides tentative evidence of species-specific trends in behaviour in response to microclimate.

The elements that make up an animal's climate are light, temperature, relative humidity, and ventilation, and these affect one another.

Light

Light can be thought of in terms of its strength (intensity) and type (wavelength). Exposure to different wavelengths of light can be important for animals. For example, providing adequate

sources of **ultraviolet (UV) light** is necessary for the health and behaviour of several species.

Some mammals (a few marsupials and rodents), birds, reptiles, and insects can actually see UV wavelengths (400–100nm), which enables them to see markings or patterns on fruits, flowers, and seeds, or within bird plumage and in urine, all of which are invisible to humans (Winter *et al.* 2003). Thus, UV vision provides an additional channel of information for those species that are adapted to see it, and they use it for functions as varied as assessing the ripeness of food or choosing a potential mate (e.g. Smith *et al.* 2002; Shi and Yokoyama 2003).

For example, the UV reflectance level of the throats of Augrabies flat lizards *Platysaurus broadleyi* has been shown to provide a signal between competing males, because those with the richest UV throats are the best fighters (Whiting *et al.* 2006). In addition, UVB (315–280nm) is associated with the synthesis of vitamin D, and affects health and behaviour, including calcium metabolism and reproduction (e.g. Cole and Townsend 1977; Regal 1980) (see also **Chapter 12** on 'Feeding and nutrition').

Unfortunately, most windows do not allow the transmission of the full spectrum of light, and as a result UVB levels are usually insufficient if animals do not have access to natural light in outside enclosures (**Fig. 6.11**). In these cases, animals need either vitamin D supplements in their food or artificial sources of UV, such as special lighting (Gehrmann *et al.* 1991; Bernard *et al.* 1989). There are many commercially available UV lights, but they should be checked regularly, because the level of UV they provide may be variable and declines over time. The extent to which animals require UV is unknown and Moyle (1989) cautions that its provision should be restricted. Reptiles from open habitats, for example, may only need 30–45 minutes of exposure daily.

Light is important not only because of its physical properties, but also because its distribution through time (photoperiod) can affect many features of animals' lives. For the majority of species, it is best practice to ensure that the photoperiod incorporates the

Figure 6.11 The provision of light to inside enclosures can be difficult to achieve because many materials prevent light penetration, especially at UV wavelengths. In this elephant exhibit at Duisburg Zoo, great efforts were made to increase the light levels and a custom-made polymer was fitted to allow UV light penetration. (Photographs: Vicky Melfi)

daily and seasonal variations for which the animal is naturally adapted. For nocturnal species, this can be accomplished by keeping them indoors on a **reversed lighting schedule**, which ensures that when it is light outside, it is dark inside.

Changes in day length can trigger the start of the breeding season, parturition, migration, and many other behavioural changes in animals (see **section 9.1.4** for more on triggers for breeding). When animals have adapted to the southern hemisphere and are housed in captivity in the northern hemisphere, behavioural changes associated with season will be reversed (and vice versa). Carefully managed lighting systems can negate circadian and seasonal discrepancies in daylight, although many animals appear to be comfortable adapting to the lighting conditions of their captive environment. There are many other factors that may vary in a period of 24 hours that affect, or contribute to changes in, observed behaviour and physiology.

For example, many hormone profiles follow a daily pattern, such as cortisol which is naturally higher in the mornings than in the evenings.

Temperature

Extremes in temperature can have deleterious impacts on animals, ranging from frostbite to heatstroke, and may also be capable of affecting welfare in more subtle ways. For example, Rees (2004) suggested that low temperatures may influence the performance of stereotypies in Asian elephants, on the basis that he found that temperature and the rate of stereotypies were negatively correlated (average temperatures measured were 9°C and 23.2°C on the coldest and warmest days, respectively); in this particular study there may also be other confounding variables leading to stereotypies. However, it is important to note the extent to which the ambient climate needs to be adjusted for specific species' needs; this is dependent on the degree of mismatch between the animals' native habitat and the zoo location. Examples of extreme mismatches are the housing of elephants in the far northern hemisphere or polar bears in Southeast Asia and Australia. For the majority of animals, well-constructed enclosures that offer protection from extreme temperatures can negate many of these challenges. This protection can be achieved indirectly with the provision of shelters, but also through artificial climate control. A disadvantage of artificial climate control systems is that they are expensive financially and, more importantly, environmentally; thus heating or cooling large areas and water bodies requires careful consideration (see **section 6.1.4**). However, temperature gradients can be achieved relatively easily through the provision of localized heating or cooling, or by altering ventilation. Localized heating can be provided with heat lamps or hot rocks, and temperatures can be kept low within inside enclosure areas by refrigerating them.

The extent to which species 'need' either hot or cold climatic conditions is debated; we know very little about the impact of climate on animal behaviour, and even less about its impact on animal welfare. For some species there are recommendations for the provision of temperature ranges; for example, the SSSMZP (Defra 2012a) recommend that most reptiles are kept at 20–35°C, and tortoises and crocodilians at 26–32°C. At these temperature levels, extra care needs to be taken with hygiene because many **pathogens** proliferate under these warm conditions, but again more research is needed in this area.

Relative humidity and ventilation

Relative humidity—that is, the result of temperature and the moisture content of the air—is a very important part of the environment for many animals. For example, African spurred tortoises *Geochelone sulcata* develop significantly taller carapace humps (considered a pathological condition) when they are maintained in low levels of relative humidity (25.7–57.8 per cent and 30.6–74.8 per cent) compared with higher levels of humidity (45–99 per cent) (Wiesner and Iben 2003).

Few studies have investigated the impact of humidity on zoo animals, so broad recommendations are suggested by the SSSMZP (Defra 2012a) for providing humidity gradients for animals such as reptiles (50–80 per cent) and amphibians (65–95 per cent). Humidity gradients are important for mammals as well. Anecdotally, a lack of humidity has been observed to result in skin problems, whereas high levels of humidity are associated with increased disease transmission.

To maintain humidity levels, misting the enclosure with water is customary. Again, it is suggested that ventilation be used to create this gradient, so that temperature and the water content of the air can remain fixed.

6.2.4 Safety

Both animals and people need to be kept safe in the zoo. Keeping animals safe is principally achieved through good enclosure design, whether this is to keep animals away from other animals or from people, or vice versa. This involves the careful planning of enclosure perimeters and accessibility to people—both keepers and the public.

Because enclosure size varies with species, so will the materials or techniques used for their perimeters or access points; barriers are explored more fully in the next section.

The level of security required is dependent on the animals' abilities (do they present a hazard, or are they thought to be dangerous?) and on the behaviour of the zoo visitors (do they respect the animals space, or will they ignore the signs that advise against certain types of behaviour?). Appendix 12 of the SSSMZP (Defra 2012a) lists all species that are considered by UK law to be hazardous and, for some of these, specific recommendations are made regarding housing. For example, venomous snakes should be housed in solid walled or roofed enclosures to prevent their escape, and to stop staff and visitors from reaching them. For many other species, there are a variety of methods that can be used to ensure that the animals can be exhibited safely and that people's safety level also remains high.

With all animal enclosures, it is sensible to consider worst-case scenarios, and to build into housing and husbandry appropriate safety precautions to limit these. All enclosures housing dangerous animals should have warning signs, whether on display to visitors or behind the scenes, and all should be individually locked. The staff service area should be free from hiding places, and protocols and staff training for shifting animals between enclosure areas is necessary. Other sensible precautions that can be taken to reduce the likelihood of escape are double doors[7] and appropriate enclosure perimeters.

6.2.5 Barriers

Barriers and/or perimeter fencing are not constructed merely to keep animals from getting out of the enclosure, but also to stop other animals and people from getting in. Although this may seem counter-intuitive, consider, for example, waterfowl which may be at risk of predation at

night from foxes and other animals; in this instance, fencing has to stop animals from getting in. Similarly, the actions of some visitors, such as providing animals with food or taunting them, could potentially harm the animals, and thus the visitors and the animals need to be kept separate.

Stand-off barriers are a simple, but effective, method of increasing the proximity between animals and visitors, the premise of which is to increase the distance between the animal's enclosure perimeter and the zoo visitor. This separation is also necessary if electric fencing is used, so that visitors are not harmed. A variety of materials can be used as stand-off barriers, including vegetation and hedges, or other fencing materials, such as metal posts.

Enclosure perimeters can be made from various materials, including horizontal and vertical posts, wire or mesh, electric fencing (or strands), moats (whether dry or filled with water), windows (glass, acrylic, or a combination), or rocks. As with all enclosure design, there are considerations that will determine the material and type of fencing used, including whether:

(1) visibility between the animals and their neighbours (animals and/or visitors) is beneficial, and therefore whether solid or partial barriers are used;

(2) the animals are able to burrow or climb, which will affect how far above and below ground the perimeter fencing must go, and whether a roof or some kind of deterrent to climbing the fence (e.g. electrics) is needed;

(3) the barrier is capable of preventing offspring from leaving the exhibit, because these are often a lot smaller than their parents.

Table 6.1 provides an overview of some of the most commonly used barriers, and their associated advantages and disadvantages from the perspective of animal, keeper, and zoo visitor.

---

[7] The term **double doors** is commonly used to describe a situation in which two doors, with a vestibule between them, separate animals from the 'outside world'.

Type	Advantage			Disadvantage		
	Animal	**Keeper**	**Visitor**	**Animal**	**Keeper**	**Visitor**
Solid*	Depending on height, provides safety Prevents disease transmission	Separates animals Prevents visitors from feeding animals	–	Can lead to injury if animals collide with it Can prevent view of surroundings May affect communication between animals	Can prevent view of the animal	Obstructs view of animals
Partial**	Can provide greater usable space	Can aid introductions	Restricted viewing can make a glimpse of an animal more exciting	–	–	Can obstruct view, although new materials are less obvious (e.g. zoo mesh) Considered 'unnatural' Does not prevent human–animal interaction
Bars	As above	Can facilitate keepers' escape from the enclosure, whether the bars are horizontal or vertical	–	–	–	Associated with negative connotations of animal welfare As above
Netting and mesh***	As above	Can accommodate any shape	Can be plastic-coated or painted to reduce visibility	Could become tangled	Metal can rust even under plastic coating UPVC can become brittle in the sun after long exposure Can be eaten through by pest species, e.g. squirrels	–

Electric	Can learn to avoid it	Easily create temporary barriers Cheap	Good visibility	Not visible so can get injured Can get entangled in it A deterrent, not 'fool-proof'	Some body parts do not conduct electricity, e.g. antlers, horns, hair	Needs to be well signed as a hazard and out of public reach
Glass	Prevents disease transmission Laminated glass provides climate control Double glazing provides noise reduction	Using acrylic and glass is very strong	Provides a good view	Close proximity between animals and visitors	Needs regular washing Expensive	Visibility can be reduced if the glass is scratched, if it is sunny (reflection), or if there is condensation
Moat	Some animals may use the water or objects in it, e.g. eat some of the plants growing in it or wade in it	Wet moats can be used as habitats for other species (e.g. plants, fish)	Provides 'naturalistic' view Invisible barrier between species	Animals can fall into the moat and get trapped Water can provide a route for disease transmission A lot of space is required, which cannot be used by the animals in most situations	Dry moats can flood Wet moats can freeze Need method to access animals and/ or enclosure safely	Increases the distance between the visitors and animals, which can reduce visibility

Table 6.1 The advantages and disadvantages of some of the more commonly used barriers in zoo enclosure design

*Materials include: wooden fence panels; brick walls; glass or acrylic; hedges, etc.

**Materials include: metal posts; electric strands; chain link; weld mesh; netting, etc.

***Materials include: metal; nylon; combinations of the two.

Note: A huge variety of barriers are incorporated into zoo animal enclosure design, which fulfil many functions, from preventing animals from escaping to restricting visitor access. The materials used will affect both their utility and their appearance.
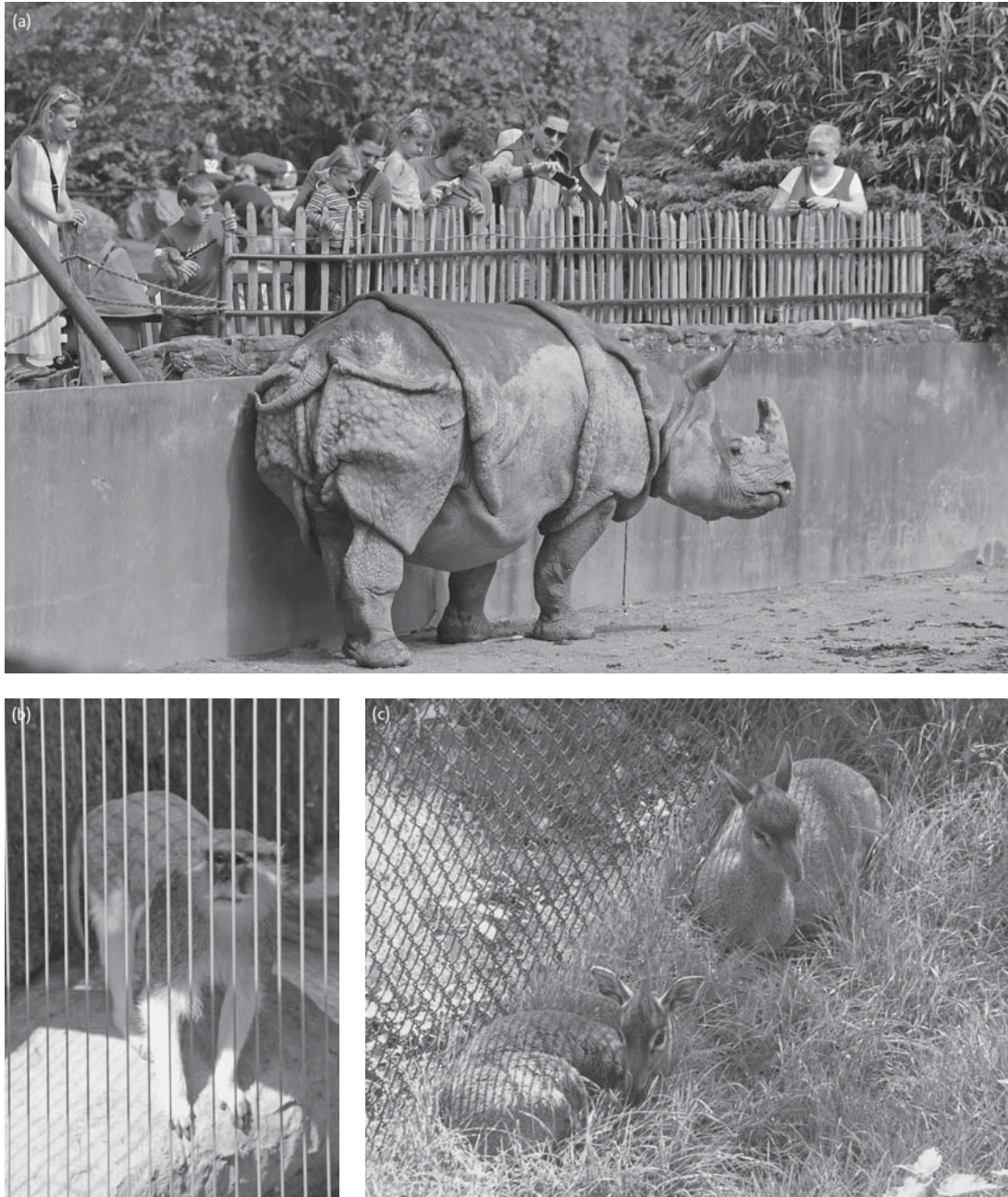
Figure 6.12 The barrier types employed in zoos are diverse, as are the materials used to construct them. Some of the more common types of barrier are (a) vertical fencing, (b) vertical wire, (c) chain-link, (d) zoo mesh, (e) rock work, (f) glass, and (g) water, in the form of moats. The safety of animals should always be considered when choosing between barriers—i.e. the likelihood of drowning in water moats could be prevented by the provision of gently sloping sides entering the water or ropes (h), which primates can use to prevent them slipping into the water. (Photographs: (a) Jereon Stevens; (b–d, f, g, h) Vicky Melfi; (e) Leszek Solski, Wroclaw Zoo)
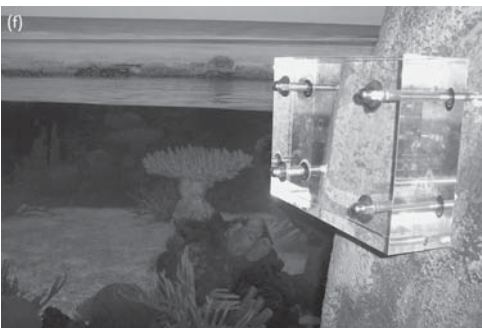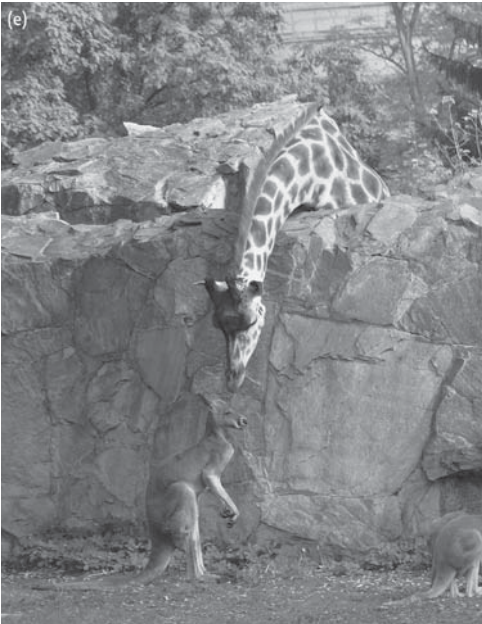
Electric fencing is available in many guises, from single-strand electric tape, to imitation grass and ivy, and electric netting and floor matting (**Fig. 6.12**). Electric fencing can be used as a perimeter barrier, and also to prevent animals from gaining access to various other resources in their

enclosure, such as high trees that they may damage, or which provide them with a vantage point from which to escape. All electric fencing should be regularly checked, should have an alternative power supply (battery) back-up, and should be attached to an alarm system that would be activated

if the electric current were to be disrupted or disconnected. It may seem obvious to mention, but electric fencing works because animals get an electric shock when they touch it. Usually, this is because the animals are on the ground and touch a 'live' wire. However, some animals may be able to leap onto an electric fence and thus will not be 'earthed', so in these situations it is essential that the fencing provides an earth, for example by providing alternate live and earth strands.

Electric fencing can be very effective at preventing predators (interloper species) from entering enclosures and is recommended by the SSSMZP (Defra 2012a), as long as adequate consideration of zoo visitor safety is adhered to (e.g. HSE 2006). Electric fencing is most effective when animals are trained to recognize it and thus avoid going near it; an electric shock acts as a punishment, which reduces the likelihood that a behaviour will be repeated (see **section 4.1.2** for a discussion of such **operant conditioning**). Different species may react differently to electric shock; for example, **Fig. 6.13** shows how three different rhinoceros species were observed to react to getting an electric shock and thus illustrates, even if anecdotally, how the same barrier method may not be suitable in all situations for all individuals or species.

Many perimeter fencing methods are not used on their own, but in combination with each other. For example, electric fencing is frequently used with mesh-style fences. When the electric fence is positioned at the top, bottom, or all over the mesh, it can prevent animals from escaping over the top of a fence, prevent animals that cannot leap from scaling the fence or from knocking it down (for example, red pandas, binturongs, and equids, respectively), or prevent animals that can leap from making contact with the fence at all (for example, primates).

Electric fencing is also used in conjunction with moats, both dry—that is, a **ha-ha** (**Fig. 6.14**)—and wet. For example, the illusion of a mixed-species paddock can be obtained by using dry moats with electric fencing running at the bottom of them, providing the visitor with a vista of different species sharing the same area. The positioning of the electric fence can determine its function, as illustrated in **Fig. 6.15**.

As with all housing and husbandry features, trade-offs are made between different barrier methods and the needs of all the stakeholders (animals, keepers, and visitors). The emphasis on naturalistic enclosures, which was discussed in **section 6.2.1**, is particularly evident in the choice of perimeter fencing chosen. It is clear from any
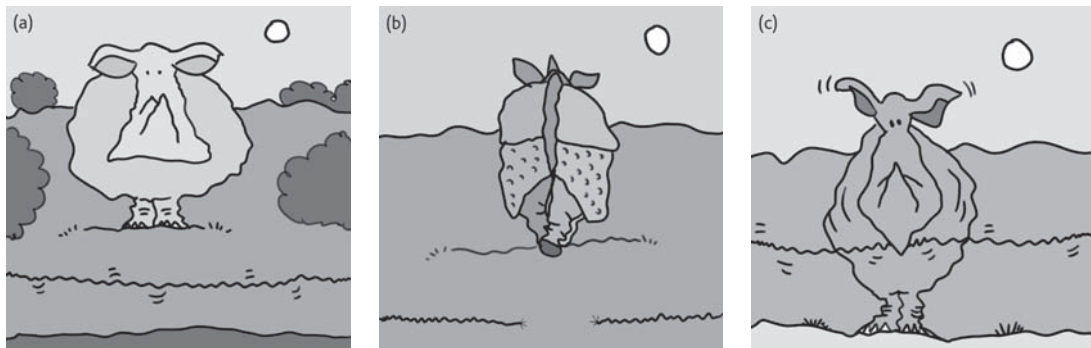
Figure 6.13 The result of coming into contact with electric fencing—having an electric shock—has been observed to lead to various reactions in different species of rhinoceros, according to Julian Chapman of Paignton Zoo Environmental Park. As illustrated in the cartoons above: (a) a white rhinoceros was seen to react as we might expect all animals to and retreat from the fence after receiving an electric shock; (b) however, an Asian rhinoceros charged straight through the electric fence, regardless of receiving an electric shock; (c) unfortunately, a black rhinoceros seemed to be unable to move after being shocked and remained stationary in contact with the electric fence. (Pictures: Phil Knowling)

Figure 6.14 Combinations of barrier types are frequently used together; this is especially true when using a ha-ha. In these two examples, the gradient and species housed in the enclosures mean that the animals are able to 'use' the ha-ha area. Escape of the animals is prevented by the steep gradient, on the visitors' side, along with (a) a standard vertical fence and (b) a very steep concrete wall. (Photographs: Julian Chapman)
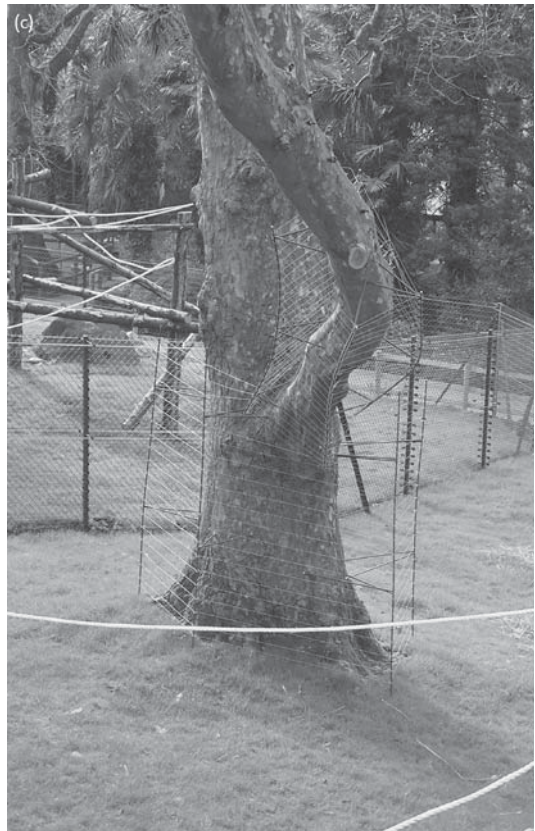
Figure 6.15 Electric fencing can be used to prevent animals from: (a) escaping—at Dallas Zoo electric fencing has been 'naturalized' by almost hiding it behind large fallen trees), (b) using parts of their enclosure (here a white-cheeked gibbons attempts to grab...who knows what, given he is on the side with the grass), and (c) destroying plants within their enclosure. (Photographs: (a and b) Jereon Stevens; (c) Julian Chapman)

casual walk around new zoo enclosures that the most commonly used perimeter fencing types are those that are aesthetically pleasing or invisible to the visitors, such as glass/acrylic, moats, and mesh.

6.2.6 Water

All enclosures, whether aquatic or not, require water (**Fig. 6.16**). Essentially, water is used by keepers to clean enclosures, for animals to drink, and may also function as a swimming pool, or for use as a barrier or aesthetic feature within the enclosure. As might be expected, the care taken on water provision and management within aquariums is far greater than when supplying water for many terrestrial species; however, the need for clean and safe provision is paramount to both.

Figure 6.16 Water is an integral part of all enclosure design; this is especially true for aquatic species, for which water makes up their entire environment. Circular aquarium tanks, called kreisel tanks (the word comes from the German for spinning top), are designed with a minimum of tight corners and internal hardware so as to avoid damage to delicate marine animals such as seahorses, jellyfish, and other zooplankton. Larger circular tanks, which hold many more animals, have now been built. A kreisel tank has a pumping system which creates a gentle circular or spiral laminar water flow, to help keep the animals suspended in the water column. Water leaving the tank passes through a fine mesh screen, again designed to minimize damage to the tank inhabitants. (Photograph: Katharina Herrmann)

Some species have specialist needs when it comes to water provision; for example, it is recommended that sufficient water is provided to reptiles and amphibians to allow them to fully immerse their bodies (Defra 2012a). The behaviour of some animals can also be dependent on water provision. A gentle slope should always be provided to ensure that animals can enter and leave water without difficulty; indeed, predominantly aquatic species should be provided with sufficient water to allow them to swim comfortably, but adequate beaching areas should also be provided where necessary.

Water quality is important and needs to be managed differently depending on whether it is an open system, a closed system, or a semi-open/ semi-closed system (EAP 2008). The needs of all species that live in or have access to the water body also need to be considered. With open water systems, it is necessary to monitor the water entering and leaving the enclosure to ensure that concentrations of chemicals are not toxic or are at non-irritant levels, to secure the safety of animals and also people (and the broader external environment). The precise checks undertaken depend on the species being exposed to the incoming water and the type of sterilizing agent or oxidant used (if they are used at all), but are likely to include salinity, pH levels, residual bromine levels, and/or chlorine; a greater array of tests need to be conducted when dealing with fully aquatic species. The SSSMZP (Defra 2012a) advise that aquarists monitor water stringently and regularly, and have on-site laboratory facilities to support this.

Water temperature should also be checked for most species, because they may react badly to sudden changes. Prolonged exposure to temperatures outside the range of those in the environment where a species naturally occurs may impact on health, behaviour, and the overall quality of life of the animals in that enclosure. Temperature can also play a role in facilitating breeding; for example, it has been suggested that grey nurse sharks *Carcharias taurus* in Australia are more likely to produce viable offspring when the enclosure water temperature fluctuates within naturally

occurring ambient harbour temperatures (Nick Boyle, personal communication). Furthermore, it is recommended that any pool used to house pinnipeds in New South Wales should ensure that temperature ranges fall within the range of those expected in the animals' natural geographic range; maximum temperatures should range between 5 and 28°C (Standards for Exhibiting Seals in New South Wales, Clause 6, Note (e) 2008).

Water is a very effective mode of disease transmission, so care needs to be taken to ensure that pathogens are kept at low levels and are not allowed to proliferate. In some jurisdictions water sampling must be performed to determine the median bacterial content of water bodies. This helps to identify sudden changes, and to maintain a system that is safer for animals, staff, and visitors; this is especially important for the latter where close contact is allowed. For example, it has been suggested that the median bacterial content in water samples (housing pinnipeds in New South Wales, Australia), must be less than 150 faecal coliform colony-forming units (CFU[8]) per 100 ml of water; if this is exceeded the water must be tested 24 hours later and if there is no change immediate steps should be taken to reduce the CFU levels to below 150 within 24 hours (Standards for Exhibiting Seals in New South Wales 2008).

In open systems, water 'cleanliness' or water quality is achieved by removal of 'dirty water' and its replacement with 'clean water'. The mode of water disposal also requires great consideration during enclosure design. Primarily, this is to ensure that water disposal does not compromise public safety through the transfer of pathogens into public waterways, but also to ensure that environmental policy is adhered to (see **section 6.2.4**). In closed systems, however, a variety of filters are used to remove any undesirable organic matter and noxious waste, and thus ensure that the water quality remains high. In a marine mammal system the expedient removal of faecal material is important; this can be accomplished

in much the same way as with terrestrial animals in land-based enclosures. Water quality can be especially compromised when housing marine species, because they produce a lot of nitrogenous waste, which can react with other chemicals in the water to produce noxious by-products, and these can increase health risks. It is also important, when cleaning ponds and tanks, that toxic disinfectant residues are removed. Similarly, adequate filtration systems are important in aquaria as fish excreta raise ammonia levels. In efficient water systems natural bacteria can be cultured to break down ammonia into nitrite and nitrates, which can be removed readily when water is changed. Ozone can be used at a low level as a microflocculent to gather small waste particles and bind them, after which they can be removed via filters. This improves water clarity.

Water management is a complex and technologically advanced topic, which has only briefly been touched on here. For zoo species that spend a large amount of their time in water it is important to strike a balance between adequate sterilization, display aesthetics, and ensuring that water chemistry is monitored and kept at safe levels. Seasonal fluctuations should be factored into the management of a life support system, and any changes in the normal operation of life support or environmental conditions such as excessive rainfall, water quality changes, run-off, algae blooms, or an increase in bio-load may warrant a change in testing frequency. There are also a variety of 'challenges' which occur when managing water systems and the animals that live in them. For example, many captive marine mammals develop eye problems and yet there is little consensus about cause, prevention, or treatment, whether it be related to water quality, enclosure design (i.e. reflection), diet, or some other factor (e.g. Koutsos *et al*. 2011).

On a larger scale, water quality management aims to simulate and provide water which reflects that found in native habitats; this is especially true for aquarists looking after fish and other aquatic species. As these systems are complicated to set up, once they are stable, efforts are made to ensure

---

[8] CFU stands for colony-forming unit, which is an estimate of bacteria and/or fungal numbers.

that they stay within a relatively tight fixed range. It has been suggested that an artefact of this captive stable environment might be the conditioning of aquatic species, which are not flexible to environmental variation. And as all environments change to some extent, aquatic animals reared in very stable conditions maybe less suitable for reintroductions, like their terrestrial cousins.

6.2.7 Housing designed to aid husbandry

So far, we have considered some basic housing requirements that are tailored to the specialist needs of different exotic species. Another basic requirement for good housing is the inclusion of structural housing features to facilitate husbandry, whether moving, restraining, or simply allowing the separation of animals. Separation areas are necessary if animals require restraint and should be regularly used by the animals so that they are not associated with fearful events. These areas are also helpful to restrict the contact between animal and keeper, because many species will need to be locked away from the area in which the keeper is working.

An appropriately constructed enclosure can also facilitate the provision of enrichment, for example by providing sturdy uprights from which enrichments can be hung, by anticipating that more furniture will be added in the future, and by making allowances for how extra furniture will be moved into the enclosure (see **Chapter 8**).

Finally, it is important to consider what requirements might be necessary in the future and build them into the design of housing; after all, a zoo may have only a pair of animals today, but next year it might have dozens more if the pair reproduce well—or the pair may no longer be compatible and may have to be housed apart from one another.

6.2.8 The furnishings

Technological advances, increased expertise in designing and building zoo animal exhibits, and a greater understanding of animals' needs have shaped changes in zoo enclosure design. It is essential that the 'basics' are included in zoo animal housing, but it is especially important that these enclosures are appropriately furnished. The provision of appropriate furnishings transforms a barren enclosure into a complex one (see **Box 6.1**).

Essentially, furnishings can include all the modifications made once the structure of the enclosure is completed. There are obviously many changes that can be made to enclosures, including those made to enhance its aesthetics (as viewed by zoo visitors), but in this section we will discuss only those furnishings that relate to animal needs.

Surfaces

The physical properties of surfaces within zoo animal enclosures are important in terms of the general maintenance of enclosures, and also because they affect animal behaviour and biology. For example, sea-bird droppings are especially destructive because they contain high levels of ammonia, which make them corrosive, so the SSSMZP (Defra 2012a) suggest that surfaces need to be durable, non-toxic, and non-porous, and to have a waterproof finish. In some circumstances, abrasive surfaces may be provided as an aid to sloughing in reptiles, and to give opportunities to wear down beaks and hooves that could otherwise become overgrown (Yates and Plowman 2004; Defra 2012a).

Similarly, softer surfaces may be more appropriate for other species, or may be necessary for the expression of certain behaviours. For example, Meller *et al.* (2007) found that rubberized flooring provided to Asian elephants *Elephas maximus* was associated with a reduction in the level of 'discomfort' behaviours expressed and an increase in standing resting behaviour, and this change in behaviour was considered beneficial because it mimicked the behaviour of wild elephants.

Agricultural housing facilities have used rubberized matting for some time to prevent sleeping sores and bumble foot (ulcerative pododermatitis, illustrated in **Fig. 6.17**), and their use for older arthritic **ungulates** in zoos is becoming more widespread. More recently, a study of bumblefoot in African penguins *Spheniscus demersus*
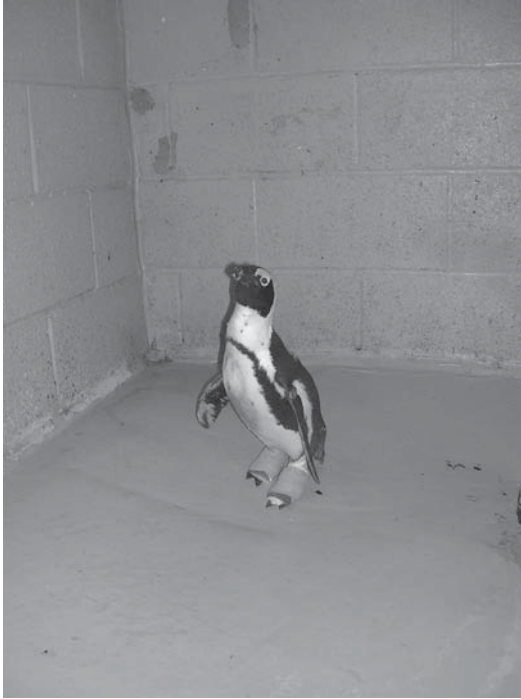
Figure 6.17 Choice of materials and substrates used in enclosure design affect more than the look of the enclosure. This penguin has developed bumblefoot, an infection associated with abrasive surfaces that cause small cuts in the feet, which then become infected. (Photograph: Mel Gage)

found that incidence was significantly higher in male penguins and those which were heavier; these two factors are likely to be confounding (Erlacher-Ried *et al.* 2012). Furthermore, low levels of swimming and a smooth concrete flooring substrate were also associated with a higher incidence of bumblefoot. Therefore, contrary to previous advice to provide smooth flooring for penguins, these data led the authors to recommend the replacement of smooth surfaces with something which would provide variable pressure and texture to the penguin's foot.

6.2.9 A room with a view

The topography of an enclosure can make a huge difference to how an animal is able to use it. Height is important to many animals so that they can express species-specific behaviours, distancing, or

flight **responses**, or simply to gain a better view of their surroundings. Height can be created with perches and platforms, and can also be provided in paddocks by using mounds of soil. The SSSMZP (Defra 2012a) suggest that birds of prey should be provided with vantage points within their aviaries so that they can have a view of their surroundings. Providing platforms and perches within enclosures is considered to enhance physical fitness (if animals use them); they also enhance welfare. For example, urinary cortisol levels drop in zoo-housed felids when the cats are provided with access to elevated areas (on the clouded leopard *Neofelis nebulosa*, see Shepherdson *et al.* (2004); on the cheetah *Acinonyx jubatus*, see Wielebnowski *et al.* (2002)). A reduction in cortisol levels is generally taken to indicate lowered stress levels and thus improved welfare, although the link between cortisol and stress levels is quite complex (see **Chapter 7** for more discussion of this).

Privacy

Many visitors to zoos will have noticed that, when provided with the choice, many animals will seek out and use areas in which they are out of sight. Why they do this is discussed more fully in **Chapter 13** on 'People in zoos', but it is clear that providing privacy within an enclosure is an important element of enclosure design. For example, Herbert and Bard (2000) found that orang-utans frequently sought out a small area at the top of their enclosure that was out of sight of the public, even though they lived in a large custom-built enclosure designed especially for them. The degree to which animals seek out privacy varies between species, and it is not surprising that species which are considered shy of people may have problems when they are not provided with enough privacy (for example, pied tamarins *Sagiunus bicolor bicolor*—see Wormell *et al.* (1996)), although much of the evidence for this is anecdotal.

Degrees of privacy can be achieved through various methods, such as allowing the animals to exit the 'show den' (the area visible to the visitors) or to hide while in the show den, or else by simply obscuring the view of the public and thus

reducing the animals' perceptions that they are 'on show'. Dense vegetation, visual barriers, or little crevices within enclosures can be successful in providing areas within an enclosure in which animals can hide.

It is obviously not ideal to have animals hiding, because zoo visitors want to see them, which is why methods developed to reduce the visibility of visitors to animals have flourished. For example, Blaney and Wells (2004) found that the use of a camouflage net, to shield gorillas at Belfast Zoo from the gaze of visitors, significantly reduced aggression and stereotypical behaviours in the gorillas, but did not prevent the public from seeing the animals. Another method, which can be seen in **Fig. 6.18**, shows how Chester Zoo used plants to increase the proximity between zoo visitors and a group of mandrills at their viewing windows. The Zoo noted that there was a reduction in the stress-related behaviours expressed by the mandrills after the provision of these plants.

A particular need for privacy is shown by parent animals when they move their offspring between multiple den sites. It is usually thought that moving offspring between multiple dens is the result of disturbance, both from humans and from other species, and could lead to a reduction in the survival of offspring. However, Habib and Kumar (2007) suggested that Indian wolves *Canis lupus pallipes* moved offspring between den sites as the pups grew, and thus it was not a result of disturbance but a naturally occurring behaviour. Laurenson (1993) also observed that wild cheetah mothers moved their offspring routinely, about every 6.6 days. Thomas and Powell (2006) considered that, among other factors, the provision of multiple den sites to captive African hunting dogs improved their reproductive success. Anecdotally, the provision of multiple den sites to other captive species appears to facilitate breeding— for example, in red pandas *Ailurus fulgens*, binturongs *Arctictis binturong*, and maned wolves *Chrysocyon brachyurus*. In addition, some parental behaviour may favour privacy from conspecifics. For example, nursing bottlenose dolphins *Tursiops truncatus* at Kolmården Wild Animal Park, Sweden, were observed to suckle their young more frequently when alone (more than 80 per cent of observations) and away from their social group (Mello *et al.* (2005).

6.2.10 Acoustic environments

An aspect of zoo animal housing and husbandry which has been previously neglected (in the first edition of this book, it only received a brief mention) is the acoustic environment that zoo animals experience (Hanson *et al.* 2012). More needs to be learnt about this subject by understanding not only the animals, but also their

Figure 6.18 Despite the greatest efforts made to ensure that zoo enclosures meet the needs of stakeholders, research can sometimes highlight areas in which this has not been accomplished. (a) At Chester Zoo, it became apparent that visitor pressure was having a deleterious impact on the behaviour of their mandrills. (b) This pressure was successfully alleviated by the use of planters placed between the visitors and the viewing windows. (Photograph: Chester Zoo)
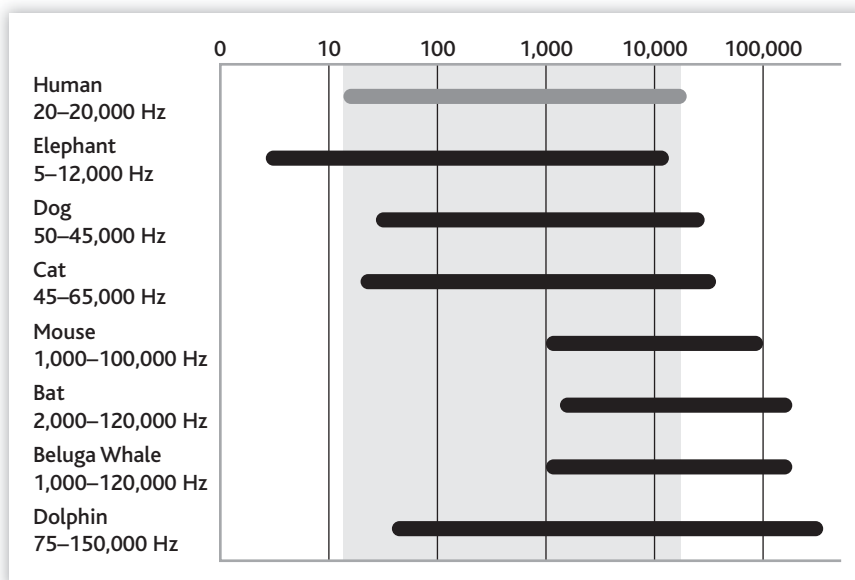
Figure 6.19 As you can see from this illustration, humans have fairly limited hearing compared with many other species. This often means that we do not appreciate the auditory world that many animals inhabit.

captive environments (see review by Morgan and Tromborg 2007). We know that there are species differences in noise perception in that all animals can hear at different and sometimes overlapping frequencies (**Fig 6.19**), although our knowledge of what different species can hear is sparse. Moreover, given the limited range which we can hear, as humans, we do sometimes forget or misjudge the acoustic environments of other species. And if we do hear what they hear, the animals' perception of the noise might still be different owing to differentials in body size and anatomy. As described in **section 7.1.1** (species differences), when weighted for the sensitivity with which rats hear, hurried laboratory husbandry tasks exceeded 90dB (Voipio *et al.* 2006), which would not be allowed in a human workplace (HSE 2006).

In a zoo environment, there are many sources of noise and disturbance, including other animals, people, construction, and when zoos host concerts, and we are probably conscious of some of these, but we possibly forget about the routine noises of gates clanging shut, and those things that we ourselves cannot hear like strip lighting or TVs on standby (Morgan and Tromborg 2007). In **section 7.3.1** ('Challenge') we note that noise from construction, concerts, and zoo visitors, led to significant changes in behaviour, which were likely to reflect compromised welfare (Keane and Marples 2003; Shepherdson *et al.* 2004). In a zoo setting, noise is likely to be qualitatively and quantitatively different, and physically and temporally different, between the zoo and the animals' native habitats, which is likely to have far-reaching consequences for behaviour and welfare. In a 'wild' setting, where increases in noise (referred to as noise pollution) constitute a smaller degree of difference compared with that experienced by zoo animals, a study showed that this noise pollution significantly affected bird behaviour and led to ecological consequences, i.e. different plants were pollinated (Francis *et al.* 2012).

In this long overlooked area of zoo animal management, there is much we do not know, but that noise is affecting the animals, possibly negatively, is likely. This is an area ripe for study, where data are needed to answer some simple and fundamental issues, of what noise is being perceived, what level of noise is being generated, and at what point does the noise generated have an impact? Can we reliably attenuate noise when and if we determine that noise levels are too high?

6.3 Husbandry from birth to death

'Husbandry' is the term used to describe the processes undertaken to care for animals and includes many routine, and also some infrequent, events. The most important point to remember when considering zoo animal husbandry is that we, as zoo professionals, are ultimately responsible for the lives of zoo animals, and determine what, how, and when many events occur in their lives, from their conception to their development (which is considered in **Chapter 9**), and, finally, how and when they die. This section will briefly outline some common husbandry practices and illustrate how these, too, need to meet the needs of the three main stakeholders: animals, keepers, and visitors.

6.3.1 Daily routine

Keepers meet the animals' basic needs of survival through effective cleaning and feeding, and by monitoring them. Some of these are discussed in more detail in **Chapter 11** on 'Health' and **Chapter 12** on 'Feeding and nutrition'. Here, we will concentrate on the need for keepers to move animals around within their enclosures routinely, in order to carry out these tasks.

It is dangerous for the keepers to interact, or to go into an enclosure, with many species, so moving the animal around has to be done very carefully. This can be achieved by using a series of different techniques, from moving into the animal's flight distance, to using operant conditioning techniques (training).

When a human walks towards an animal, it will often appear unaffected by the human's presence until he/she gets too close, at which point the animal may stop whatever it was doing. If the human continues walking, the animal will eventually either move away from or threaten him/her, and at this point the human will know that he/she has entered the animal's flight distance—so called because invading this space will make the animal

take flight. An understanding of flight distance can be used very effectively to move animals—but it needs to be implemented calmly and slowly, because invading an animal's flight distance quickly or aggressively can result in injuries to animals and keepers alike.

Cues and commands can also be given such that the animal learns that it will be rewarded if it displays the right behaviour. In this way, operant conditioning is achieved and can sometimes take place without either party realizing it. For example, if keepers want to get an animal to move to an inside enclosure, they will frequently provide food or treats inside, so that when the animal goes inside, it is positively rewarded for coming in. This is **positive reinforcement training (PRT)** (see **section 13.4.1**; illustrated in **Fig. 6.20**), which will increase the likelihood of the animal coming inside in the future when the keeper needs to move it. Alternatively, the keeper could have moved into the animal's flight distance, shouted at it, or physically moved it. In this scenario, the animal would have moved inside to avoid the keeper and so this would represent a punishing episode, and would reduce the likelihood of the animal staying outside when the keeper needed to move it inside. As such, training is, to some extent, inherent in most daily routines.

6.3.2 Infrequent events

Many planned and unplanned infrequent events occur during the lifetime of an animal. Again, some of these events are discussed more fully in other chapters; for example, health checks and making provision to identify animals individually (through transponders or tags) are dealt with in **Chapter 11** on 'Health' and **Chapter 5** on 'Animal identification and record-keeping', respectively. In this section, we will consider introducing animals to one another and transporting them, whether within a zoo or between zoos.

Introductions

The movement of individuals into and out of groups is a frequent occurrence in many 'wild'
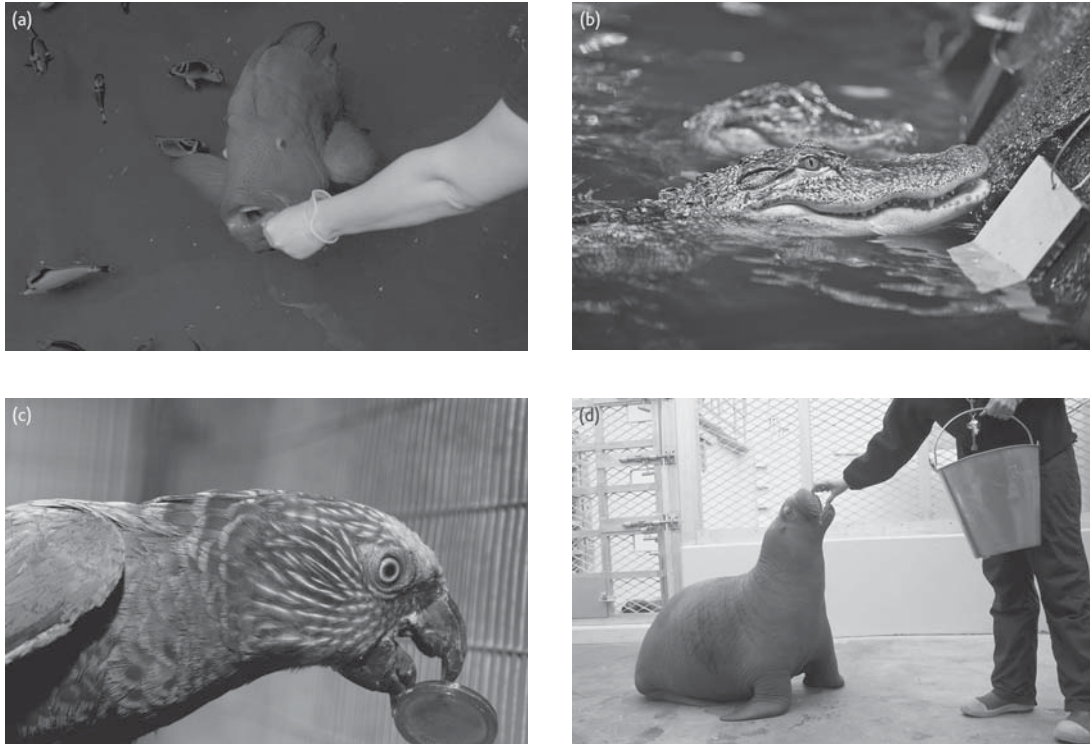
Figure 6.20 All animals are capable of learning, and the principles that underpin learning are universal to them all. This means that husbandry training, which is based on learning theory, can be achieved with all species maintained in zoos: (a) fish, (b) reptiles, (c) birds, and (d) mammals. (Photographs: (a) Phil Gee; (b) Randers Regnskov (Odense Zoo); (c) Jessie Cohen/Smithsonian's National Zoo; (d) Vicky Melfi)

social groups (e.g. Pusey and Packer 1987), in which it has evolved, among other things, to reduce the risks of related individuals breeding and having inbred offspring. These are situations that also need to be avoided in captive populations, so recommendations to move animals between groups are routinely made for all animals that are part of **captive management programmes** (**Chapter 9**). However, trying to simulate natural migrations in captive populations is associated with potential risks due to aggression and injury, even though it enables the genetic management of the population and social stimulation (Visalberghi and Anderson 1993). Because of this, alongside the genetic merits of potential breeding animals, there are many other considerations that also need to be made when considering the transfer of animals between groups—not least the logistics of doing it (Lees 1993; Norcup 2001).

There is no guarantee that, because two animals (or a new animal and a group) are genetically compatible, they will get on with each other when first introduced. In fact, it is always advisable to have a contingency plan in case an introduction has problems, and the process should always proceed slowly. Depending on the species, there is a series of steps that can be employed to enable the animals to become familiar with one another before the introduction, such as sharing the bedding and furniture of the animals that are to be introduced, or allowing visual contact and then restricted tactile contact until, eventually, they are mixed together. Kangaroo rats *Dipodomys heermanni* are a solitary species, but compatibility between pairs, and thus breeding success, improves if potential mates are kept in long-term sensory contact with one another (Thompson *et al.* 1995).

Interestingly, and not particularly conventionally, the scents of two male meerkats *Suricata suricatta* being introduced to one another was reported to be masked by the use of a strong-smelling cold treatment (Vicks VapoRub) (*Lancaster News* 2007). Because no aggression was observed, it was reported that the strong smell facilitated the introduction of these notoriously aggressive and territorial animals. A similar approach—masking animals' naturally occurring channels of communication—was used in a laboratory facility to improve the success of pairing vervet monkeys *Cercopithecus aethiops sabaeus.* Gerald *et al.* (2006) were able to demonstrate that male vervet monkeys paired together were more likely to be aggressive to one another if their scrotal sacks were similar in colour (pale or dark). As such, they were able to reduce aggression by pairing males of different scrotal sack colour, for example pale with dark and vice versa.

Although temporary modifications can be made to the way in which animals view each other during introductions, it is essential that, when enclosures are designed, ample facilities are built into the enclosure. At the very least, separate areas should be provided for both new and occupying animals.

Transporting within and between zoos

There are two main considerations involved when moving animals: one is to meet the regulations that govern live animal transport, and the other is the physical process of moving the animal.

The regulations that govern live animal transport between zoos are dependent on the species being moved and where it is going; this topic is dealt with in more detail in **Chapter 3**. The practical side of moving animals, however, involves a series of steps that need to be carefully planned to ensure keeper and animal safety, to prevent the risk of the animal escaping, and to reduce the likelihood of any deleterious impact on welfare (**Fig. 6.21**).

There has been an increase in the number of studies on the effects of transport on the welfare of animals, but most of them have focused on domestic breeds (e.g. Thiermann and Babcock 2005). Many of these studies demonstrate that transporting animals, whether by sea, land, or air, can reduce their welfare (Broom 2005; Norris 2005), although there is evidence that providing enrichment during transport can mitigate some of the deleterious signs of transport, for example in pigs (Peeters and Geers 2006).

Because of the results from these farm animal studies, we would expect that the impact of transport on zoo and other wild animals may also be detrimental, and the limited evidence supports that view. Long-tailed macaques *Macaca fascicularis*, for example, show elevated stress responses during air transport and do not return to pre-transport behavioural profiles in their new homes for some time (certainly, for more than a month) after transport (Honess *et al.* 2004). Similarly, tigers *Panthera tigris* subjected to a simulated move showed faecal cortisol peaks of 239 per cent above baseline three to six days after transport, and took nearly two weeks to return to baseline levels (Dembiec *et al.* 2004). In this latter study, there were indications that prior exposure to some of the aspects of transport could reduce the effects of transport stress. Nevertheless, it is clear that every effort should be taken to ensure that all events that take place before, during, and after transport are carried out with care and with the animal's welfare as the foremost concern.

6.3.3 The management of social groups

It is generally accepted that maintaining successful captive social groups that are similar to those that occur 'naturally' is a goal that zoos should try to attain (Hediger 1955; Hutchings *et al.* 1978). But achieving this requires an understanding of the structure and function of animal groups, as well as what factors affect them and how. For example, it is customary in the wild for males or females to leave their natal group upon maturation and find another group to join, because this reduces the risks of **inbreeding**. But carrying out transfers between groups and other social processes in a captive setting may be limited, and could thus lead to problems. Indeed, providing the animals
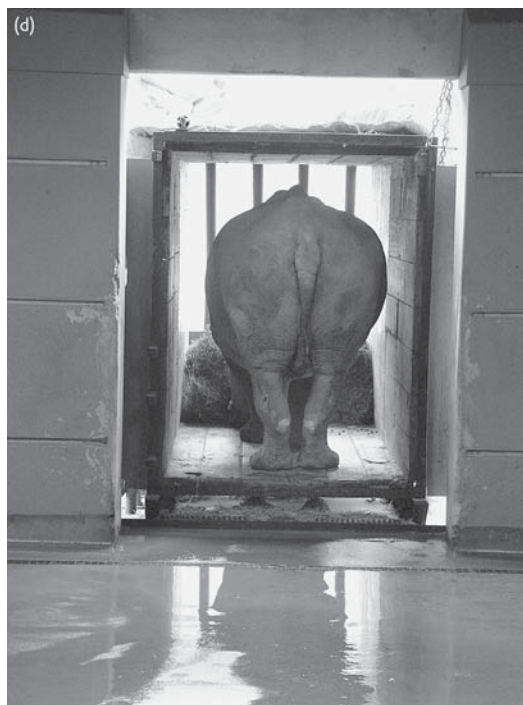
Figure 6.21 Moving animals is a complex matter, not least because the size of some animals makes the logistics more difficult in every way. (Photographs: (a) Taronga Western Plains Zoo; (c) Leszek Solski, Wroclaw Zoo; (b and d) Paignton Zoo Environmental Park)

with appropriate opportunities to enable them to express social behaviour and then manipulating this in captivity can be very problematic, because any mistakes that are made could result in a failure to reproduce or lead to fatal fighting (Visalberghi and Anderson 1993). Animals that do not move from their natal group may become the target of aggression; alternatively, introduced unrelated animals may be the focus or cause of aggression. For example, high levels of infanticide were recorded in a large captive group of collared peccaries *Tayassu tajacu* (Packard *et al.* 1990). When aggressive events were observed, it was unrelated females that were seen to attack neonates and related females that defended them. Despite the fact that collared peccaries form large social groups in the wild, it seems that, in captivity, it is necessary to ensure that females are related to reduce the likelihood of aggression.

Managing social groups is frequently considered to be one of the most important, but most difficult, tasks to achieve in captivity. This not only involves large groups of animals; solitary species must have social management as well, because they will need to be brought into contact with other individuals for breeding and will inevitably be housed near other animals. Dysfunctional social groups have negative consequences for the three main stakeholders in housing and husbandry that we identified at the start of this chapter:

- The animals themselves may experience stress, low reproductive output, or impaired immune function, or they may develop 'abnormal' behaviour patterns and aggression, some of which can be fatal.

- Keepers may find it difficult to carry out daily routine tasks successfully, because some, or all, of the animals may cease to move around the enclosure as normal.

- Visitors do not want to see animals fighting, but want to see positive social interactions.

A number of factors limit a zoo's ability to hold natural social groupings. These include space (because, if this is limited, large groups cannot be maintained and this affects the extent to which breeding can be promoted and managed within the population), individual (or species) compatibility (because, if animals do not get on and are aggressive to one another, smaller groups may have to be maintained through necessity), and animal availability (because captive populations of some species are sometimes small and so larger groups cannot be created). It is also likely that the social group dynamics will change over time, whether due to animals ageing and behaving differently, or because offspring are born. Certainly Baker (2000) noted that older (i.e. aged 30–44 years) female chimpanzees *Pan troglodytes* were less aggressive and used their enclosure less than younger (i.e. aged 11–22 years) females, while the opposite was true in male chimpanzees.

In the rest of this section, we will look at some of the techniques and processes associated with management of social groups in zoos.

Group size/stocking density

There are some species that live in quite large groups in the wild, but for which attempts to re-create large groups in captivity could cause problems if space is limited. The relationship between space and group size is referred to as stocking density, which is the number of animals per unit space. As long as large groups are given appropriate space, they will not suffer the effects of crowding and, in fact, many species thrive in large social groups. Studies have demonstrated that large group sizes are associated with significant elevations in orang-utan activity (Wilson 1982) and increases in reproductive success in Chilean flamingos *Phoenicopterus chilensis*, which require at least forty birds to breed, and Caribbean flamingos *Phoenicopterus ruber ruber*, which require over twenty birds (Stevens 1991; Pickering *et al.* 1992).

Clearly, stocking density needs to be carefully monitored, because crowding compromises animal welfare. This can result from increased competition between the animals for resources, which can lead to some animals getting no, or

little, food or shelter. Different methods of feeding or resource provision can overcome this problem to a limited extent (see **section 12.7** on food presentation).

Crowding can also lead to changes in the physiology and behaviour of the animals, as they attempt to ameliorate increased social pressures but are unable to distance themselves from one another. For example, a large group of Hamadryas baboons *Papio hamadryas hamadryas* (over the five year study period, a maximum of eighty-three and minimum of forty-six individuals) at Paignton Zoo Environmental Park was transferred to a smaller off-show part of their enclosure (measuring 3m³) from the outside area (measuring approximately 35m × 15m × 13m), so that it could be cleaned daily. Stress, measured as the performance of self-directed **displacement behaviours**, rose significantly in this group over the study period as a result of this increased stocking density (Plowman *et al.* 2005) (**Fig. 6.22**).

Social problems resulting from crowding—for example, when high levels of aggression or stereotypies are displayed (de Waal 1989)—can be mitigated with enrichment. Providing bark as a deep-litter substrate in the small off-show area of the baboon group mentioned above significantly increased levels of play and reduced aggression in the animals.

Finally, the risk of health problems increases in parallel with stocking density (e.g. Goossens *et al.* 2005) (see **Chapter 11** on 'Health'), not only because the potential disease carriers increase, but also because contamination is facilitated by both the increased proximity between individuals and the greater quantity of faeces being produced. This is true of both terrestrial and aquatic environments.
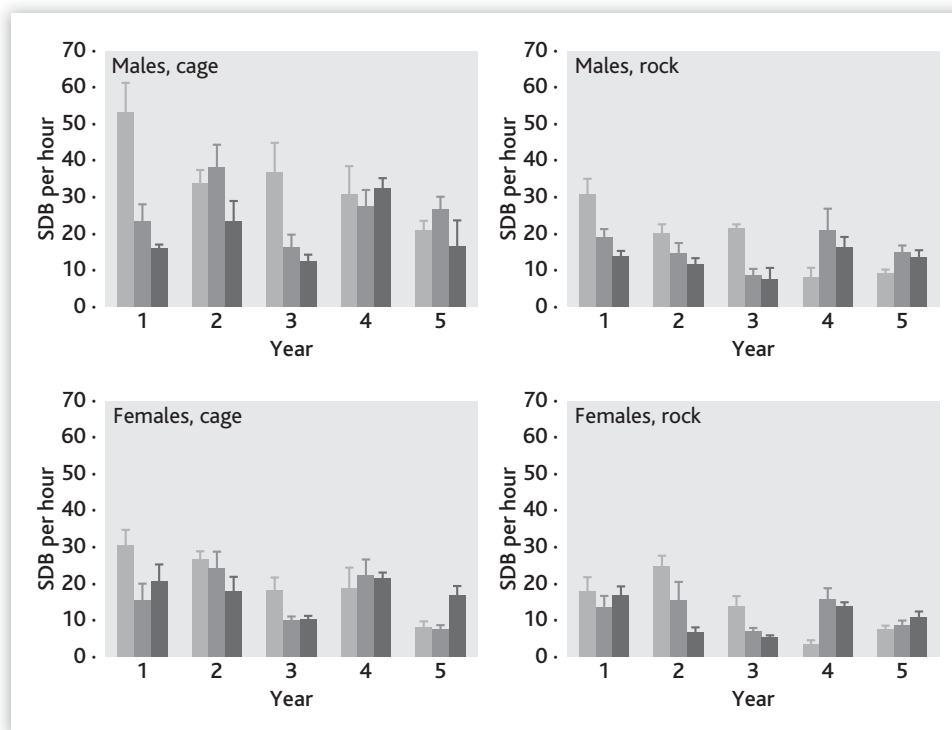
Figure 6.22 To manage a large group of Hamadryas baboons at Paignton Environmental Park, it is necessary to move the animals from their large enclosure (rock) to a smaller area (cage) so that the rock area can be cleaned. This move increases the stocking density of the group and, subsequently, an increase is observed in the mean rate of self-directed behaviour (SDB) (Plowman *et al.* 2005). The relationship between self-directed behaviour and welfare is addressed in **section 4.4**. (From Plowman *et al.* 2005)

Single-sex groups

There are a variety of different social systems and group structures in wild animal groups (see **Table 9.1**). However, attempting to replicate some of these 'natural' social groups in captivity can contribute to a surplus of animals, such as the offspring from family groups or maturing males that are excluded from harem systems by more dominant animals (Graham 1996). Some of the problems caused by surplus animals are discussed further in **Box 9.8**.

One way of preventing surplus animals is forming single-sex groups and thus limiting breeding. An example of this can be seen in the management of the Rodrigues fruit bat *Pteropus rodricensis*, in relation to which the European species management programme (EEP) has recommended that many of its member zoos hold either all-male or all-female groups to ensure that the population does not continue to grow. Similarly, in the western lowland gorilla *Gorilla gorilla gorilla*, breeding groups are composed of single adult male harems, so, as males get older, there is no place for them within the group. The European species management programme (EEP) for gorillas has recommended that some member zoos hold all-male bachelor groups as a reservoir for these surplus males.

Single-sex groups have been successfully managed for a variety of species, including blackbuck, ruffed lemur, many reptiles, and flocking birds. Indeed, maintaining a group of male cheetah *Acinonyx jubatus* to present to a potential female mate may even improve the chances of successful breeding (Caro 1993).

However, some problems can arise in captive single-sex groups. This may be because the species does not form single-sex groups in the wild or, if it does, they would be transitory or the individuals in the group would tolerate only close relatives (for example, on *Gorilla gorilla*, see Pullen (2005)). Male–male aggression in bachelor groups is of particular concern.

Unfortunately, there do not appear to be any standard 'rules' that can be applied to reduce the likelihood of aggression with all species. For example, levels of male–male aggression have been observed to be high in chimpanzees when there is a large discrepancy in age or social experience (Alford *et al.* 1995). Differences in coloration can also lead to increased aggression, as described previously in male–male introductions of vervet monkeys (Gerald *et al.* 2006). Techniques suggested to alleviate the likelihood of this aggression include slow introductions (see above) and matching behavioural profiles to increase the likelihood that animals will be compatible (e.g. Kuhar *et al.* 2006).

Although there is a need for single-sex groups in captivity, the long-term stability of these groups is not always certain, especially when considering non-related animals, the maturation of adolescents, and the movement of animals in and out of the groups (Matthews 1998; Asvestas and Reininger 1999; Fàbregas and Guillén-Salazar 2007). In addition to the possible behavioural problems that may compromise bachelor groups, the absence of young animals from single-sexed groups may also make this type of exhibit less attractive to zoo visitors and, consequently, few zoos may be willing to hold all-male groups.

Mixed-species groups

Many animals form mixed-species associations in the wild, where these associations may confer benefits such as a reduced threat of predation, improved foraging opportunities, improved social stimulation, and reproductive enhancement (Noë and Bshary 1997; Wolters and Zuberbuhler 2003; Griffin *et al.* 2005). The benefits of creating **mixed-species exhibits** (thus mixed-species associations) in zoos are considered to include the provision of:

(1) dynamic social stimulation (Thomas and Maruska 1996);

(2) a more efficient use of enclosure space, for animals which have different ecological requirements as they can use different areas within the available space (Dalton and Buchanan-Smith 2005);

(3) a higher-quality educational experience, because biogeographically representative species may be put together, or other combined groups can be assembled of animals that share other characteristics, such as waders that come from similar habitats but different continents.

However, care needs to be taken when putting different species together. Choosing species with different ecological niches within a similar habitat can reduce the likelihood of competition and thus aggression (Thomas and Maruska 1996). For example, naturally sympatric species such as **callitrichids** have been housed together in many combinations (for example, Goeldi monkeys *Callimico goeldii* and pygmy marmosets *Callithrix pygmaea*—see Dalton and Buchanan-Smith (2005)). But some naturally occurring associations do not work in captivity, or require special housing and husbandry considerations. For example, when mixing waterfowl and mammals (i.e. deer, or other ungulates), an area of land should be provided for the sole use of the waterfowl so that they are not excluded from using land by more dominant larger species. This can be achieved by excluding the ungulates with fencing (at 30cm above ground—see Defra (2012a)).

6.3.4 When should we intervene and what should we do?

Some zoo animal husbandry activities are controversial. Few people would debate the merits of conserving species or ensuring that zoo animals should have good welfare, but the husbandry techniques employed to reach these goals are frequently debated. It seems that the extent to which zoo professionals should intervene in the lives of the animals in their care can be a very contentious issue. The activities that fall under this banner are diverse and include the management of surplus animals through the use of **euthanasia** and contraception (see **section 9.7.4** and **Box 9.8**), whether we should hand-rear animals (**Box 9.6**), and the extent to which animals should

be modified, intentionally or otherwise, to suit their captive situation.

As we have already seen, the behaviour, morphology, and genetics of captive animals can change over generations in comparison with wild conspecifics. Many of the different housing and husbandry techniques that occur in the lifetime of an animal can affect it and its welfare, either directly or indirectly. For example, physical modifications to a bird's wing, termed **flight restraint** techniques, directly stop it from flying, but an overly small enclosure can also prevent it from flying.

Whether these activities should take place, when they should occur, and how they should be executed are all topics of debate, and, to some extent, whether they are contentious or not depends on whether or not you agree with them. The most that we can do here is to provide a framework to use when considering different husbandry techniques. It is important to consider the merits and drawbacks of the proposed techniques, what are the alternative techniques, and what the repercussions would be of not intervening.

Let us look in greater detail at the issue of flight restraint.

Flight restraint

Why would we want to keep birds that could not fly in the zoo? One answer is to conserve them, as part of captive management programmes, and to prevent them from becoming extinct in the wild. It is argued that it is not always possible to provide a bird species with the adequate enclosure space necessary to enable it to fly; physical space may be limited and so may the funds necessary to build larger 'roofed' enclosures. There are also reports that birds that are able to fly are more susceptible to injuring themselves in some enclosures.

It has been argued that preventing the extinction of bird species through captive management programmes is more important than the potential negative ramifications of restricting flight in some birds. The argument is that the impact of restricting flight is dependent on the extent to which the birds would ordinarily fly—or, in other words, the extent to which the bird is motivated to fly. Previous

studies have considered that behaviours that oc-
cupy a large part of animals' **activity budgets** are
necessary and highly motivated (Bubier 1996). But
Mason *et al.* (2001) demonstrated that animals
may be highly motivated to perform behaviours
that have relatively short durations. This issue is
difficult to resolve without adequate empirical data.

The alternative viewpoint is that wilfully ampu-
tating a healthy animal (such as tail docking, cas-
tration, etc.) and preventing it from performing a
natural behaviour (flying, reproduction) is abhor-
rent and compromises its welfare (see **Chapter 7**).

Discussions of this type often operate on two
levels: one that uses information gained as reli-
ably recorded and interpreted facts, and the other
based more on conjecture, assumption, or belief.
As discussed in **Chapter 7**, the need for objective
insight is essential when trying to tease apart the
emotive elements of a contentious issue. We need
to consider whether the implementation of flight
restraint affects bird welfare or conservation. This
will, of course, depend on the species and the
method of flight restraint used.

Various methods are employed to render a bird
incapable of flying. Techniques vary in terms of
how invasive or permanent they may be. **Wing
management**, especially **pinioning**, is probably
the most debated aspect of flight restraint and
works on the principal of unbalancing the bird so
that it cannot fly, or making it physically unable to
use it wings (the more common procedures em-
ployed are illustrated in **Fig. 6.23**). Feather clip-
ping is achieved by cutting through the primary
feathers from one wing to unbalance the bird. The
same is achieved with brails, which consist of a
loop of material over the shoulder of one wing,
twisted to keep the wing closed.

Surgical methods of wing management are also
available and considered by law to be 'mutilations',
defined as any '*procedure which involves interfer-
ence with the sensitive tissues or bone structures of
an animal, other than for the purpose of its medical
treatment*' in section 5(3) of the Animal Welfare
Act 2006. Within this Act, surgical procedures of
wing management are exempt for conservation
activities and listed as permitted procedures if
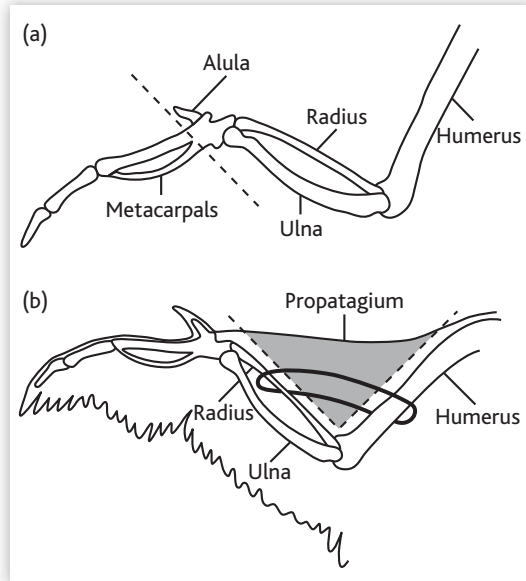
Figure 6.23 Two surgical techniques that can be used
to prevent flight in captive birds are illustrated here:
(a) pinioning; (b) patagiectomy. Whether zoos should
restrict the flight of birds and which methods should
be employed is a highly controversial topic, although
it should be remembered that, by definition, captivity
restricts the movement of all animals to some extent.

undertaken by a vet or following strict codes of
conduct. The subsequent Mutilations (Permit-
ted Procedures) (England) (Amendment) Regu-
lations 2008 provide further clarification, and
specifically allow the wing- and web-tagging of
non-farmed birds for conservation purposes,
including captive management programmes.

There are two main surgical methods.

- Pinioning, which essentially involves the am-
putation of a digit at the wing tip, although
there are variations in technique, and is legal in
the UK as long as the bird is not housed on, or
the procedure is undertaken on, agricultural
land (The Welfare of Livestock (Prohibited
Operations) Regulations 1982).

- patagiectomy (or tendonectomy), which ren-
ders the wing functionless by the removal of
all, or part, of the propatagium ligament or
the tendons of the carpal joint and gives the
appearance of a bird with an intact wing.

Aside from wing management, flight can also be restricted or prevented by:

- tethering, which is used most frequently with birds of prey and involves restricting the bird's activity by fixing it via leather straps (jesses) on its legs to a stand or post;

- overfeeding, so that the bird is too heavy to fly;

- enclosure design, because enclosures that are small can inhibit flight in larger birds if they do not have enough space or height to attain lift-off.

The SSSMZP (Defra 2012a) recommend that tethered birds must be flown at least four times a week, unless ill, and should not be tethered all year. It is also recommended that owls and vultures should not be tethered, but trained to fly from pens (Defra 2012a).

Little research has been undertaken that specifically investigates the impact of flight restraint on bird welfare and/or conservation. Hesterman *et al.* (2001) assessed the welfare implications of different flight restraint techniques by considering how they might contravene the five freedoms. **Table 6.2** outlines some of these arguments. But, because of this lack of research, most arguments that are made for or against this husbandry technique are based on the observations of experienced keepers and managers. Indeed, in most situations in which it is necessary to decide whether or not to intervene, there is likely to be little data available to inform any decision, which is why some of these issues become long-standing debates.

Should the ability of birds to fly be prevented or restricted in zoos? If flying is considered a fundamental part of their behavioural repertoire, can they live without it and what effect does that have? These are the types of question that need to be addressed when considering the costs and benefits of implementing this and other husbandry measures. (Cost–benefit analyses are explained more fully in **section 7.5.3**.)

6.4 Studying how housing and husbandry affect captive animals

Much zoo-based research investigates topics related to housing and husbandry, and whether changes in these affect animal biology, lead to an improvement in conditions for zoo animals, or help the attainment of the zoo's goals (Eisenberg and Kleiman 1977; Hutchings *et al.* 1978; Schaaf 1984; Kleiman 1992, 1994; Seidensticker and Doherty 1996). **Chapter 14** discusses what research in zoos entails, but the following section focuses on and outlines some of the different approaches that can be employed to evaluate zoo animal housing and husbandry.

6.4.1 Bottom-up or top-down?

Two different approaches can be adopted to study the effect of housing and husbandry on captive animal biology, and these are best described as 'bottom-up' and 'top-down'. The predominant approach taken is bottom-up, which is based on making speculative changes to housing and husbandry routines until the animal's biology is modified. For example, we might suspect that some element of housing and husbandry is stimulating stereotypies in an animal. In that case, we might make various modifications to housing and husbandry until we can reduce or eliminate stereotypies. This bottom-up approach has been the basis of much environmental enrichment research (Chamove 1989).

Alternatively, the top-down approach attempts to identify which factors affect captive animal biology and to what extent. This information is then used to make subsequent modifications to housing and husbandry. Using the above example, if we were trying to find the cause of stereotypies so that we could reduce or eliminate their expression, the top-down approach would be to collect information on a variety of factors, such as genetics, **nutrition**, housing, and husbandry, and then evaluate whether and how these contributed to

Method	Temporary (T)/ permanent (P)	Advantages	Disadvantages
Small enclosure	T	Able to extend full wings and preen	Potential for crowding and lack of space may restrict physical exercise
Feather clipping	T	Easy to implement	Stress from repeated handling and catch-up Irritation Development of self-mutilation Algal growth in waterfowl Excessive bleeding if growing feathers are cut
Overfeeding	T	Able to extend full wings and preen	Health and condition problems associated with obesity
Tethering[1]	T	Given flying opportunities	Lack of space may restrict physical fitness and behavioural expression
Brailing[2]	T	Flight	Long-term muscle atrophy (although apparently reversible) Impaired wing growth
Pinioning[3] Tendonectomy	P	Wings appear normal	Carrying dysfunctional wing Patagiectomy can take a long time to heal
True for all measures	P	Large social groups[4] can be more easily maintained in enclosures that are less expensive to construct and which stimulate dynamic expression of social behaviours Might reduce risk of injury from the enclosure and escape of non-native species into habitats surrounding zoo grounds	Increased risk of injury from lack of balance, or from cage mates, because less able to avoid aggression The expression of some behaviours will be restricted, e.g. ability to escape, roost, preen, and potentially mate; the latter may lead to reduced breeding success[5]

Table 6.2 The potential advantages and disadvantages associated with some flight restraint methods, with examples of worst- and best-case scenarios

[1]Owls and vultures should not be tethered (Defra 2012a).

[2]If brails are used for longer than two weeks, they should be alternated between wings to reduce stiffening of the wing (Ellis and Dien 1996).

[3]Should occur when birds are very young, at about three days old (reviewed by Hesterman *et al.* 2001).

[4]Pickering *et al.* (1992) found that a minimum of forty Chilean and twenty Caribbean flamingos should be grouped together to ensure breeding success.

[5]Data suggest that flight-restrained flamingos have less successful reproductive lives (Farrell *et al.* 2000).

Note: Temporary measures are reversible; thus, if the conditions under which the bird is housed change, the decision to restrict its flight can be re-evaluated. On the other hand, permanent measures limit the number of times that the animal needs to be caught and handled to maintain flight restriction, but are more likely to be associated with post-operative infection and pain during, and after, the procedure.

the expression of the stereotypies observed (Montaudouin and Le Pape 2005).

The two approaches can complement one another, because the 'top-down' approach can be used to identify factors that affect captive animal biology; the extent to which these factors affect the animals can then be measured by manipulating them until a change in the animals is observed. Both approaches can reveal similar information, but the bottom-up approach is less comprehensive, because the goal is only achieved if and when a change in captive animal biology occurs. As such, the study may be terminated after only one successful modification to housing and husbandry when, in fact, various housing and husbandry indices are affecting captive animal biology. The 'top-down' approach, on the other hand, provides a greater appreciation of how different housing and husbandry factors affect behaviour, although this approach is more complicated and will require more time to undertake.

6.4.2 Single-site versus multi-zoo studies

Single-site studies are defined as those that are carried out at one location (that is, in one zoo enclosure). Usually, this style of study compares captive animal biology before and after an event (a modification to housing and husbandry) to evaluate its repercussions. A typical method used to evaluate the impact of housing and husbandry changes is post-occupancy evaluation (POE) (see **Box 6.2**).

A major benefit of this approach is that it will reveal how housing and husbandry factors affect captive animal behaviour in that enclosure; these studies are also relatively cheap, quick, and easy. In these situations, extraneous variables should not confound the results as they are matched between treatments. Order effects and those contributed by the passing of time can be reduced through design modifications—for example, using a Latin square design or randomization between conditions (Lehner 1998). Unfortunately, single-site studies usually suffer from having a small sample size, which may be further reduced if subgroups,

such as sex–age classes, exist within the group (see **Chapter 14** for more on dealing with small sample sizes in research).

A drawback of single-site studies is that they are of limited use when considering how housing and husbandry factors affect animals elsewhere—in other enclosures or in other zoos. The results do not lend themselves to generalizations to other animals or species, although studies of this type cautiously predict ramifications in other circumstances (Carlstead *et al.* 1991; Baker 1997). By making changes to food presentation, enclosure structure, and visitor numbers in one zoo, studies have been undertaken to investigate their impact (McKenzie *et al.* 1986; Smith *et al.* 1989; Mitchell *et al.* 1991a).

Alternatively, multi-zoo studies, which compare one species across several zoos, provide the opportunity to investigate much more about the implications of changing housing and husbandry (Melfi and Hosey 2012). For example, in a complex enclosure, the addition of another substrate (e.g. a log) may have less effect than if it were incorporated into a more barren enclosure. Other studies have used this method to evaluate how housing and husbandry affect reproductive success, activity levels, and enclosure use (Ogden *et al.* 1993; Mellen 1994). Unfortunately, multi-zoo studies are seldom conducted, despite their benefits, probably because they require more resources than single-site studies (Mellen 1994). More details are given about multi-zoo research studies in **Chapter 14**, including the use of surveys and the Methods of Behavioural Assessment (MBA) projects, which have been incredibly useful for identifying the relationships between behaviour, housing and husbandry, mortality, and reproductive success (Kleiman 1994; Carlstead *et al.* 1999a; 1999b).

6.5 Guidelines and housing and husbandry recommendations

Housing and **husbandry guidelines** that refer to zoo animals are compiled by a variety of agencies with differing degrees of comprehensiveness. Within the UK, the SSSMZP (Defra 2012a) is

Box 6.2 POST-OCCUPANCY EVALUATION

Post-occupancy evaluation (POE) was developed to assess how people used and interacted with their environment. Within a zoo setting, POE provides a valuable tool with which to evaluate how different species behave in their enclosures and use the different resources within it. For example, Chang *et al.* (1999) studied the enclosure usage by mandrills *Mandrillus sphinx* before and after major changes to their enclosure. They were able to determine that enclosure refurbishment had led to a significant change in the mandrills' behaviour, which resulted in them expressing behaviour that more closely matched that of their wild conspecifics (see **section 4.5.3** for more on this study). Equally, POE techniques can explore an animal's interactions with the environment over time, thus enabling us to evaluate how long an enclosure may stay stimulating after enrichment or refurbishment, or if this enclosure is new. This information is essential when considering the best time at which to make changes to housing and husbandry.

An example is a study of red river hogs *Potamochoerus porcus* at Paignton Zoo Environmental Park. It was obvious that these animals had devastated their new enclosure from the moment they were put in it. Initially, it was overgrown with shrubs and trees, but, very quickly, the hogs had chewed, rooted, and foraged away at this vegetation until little was left. POE provided data which demonstrated that, in their first three months in the new enclosure, all three animals used the area available to them at significantly lower levels than when they first entered the new enclosure (Dayrell and Pullen 2003). This information enabled a change in husbandry to be introduced: a far-reaching **scatter feed** that increased the hogs' use of the enclosure back to the levels observed when the enclosure was new and interesting (**Fig. 6.24**).

POE can measure how the animal's behaviour or enclosure use changes, or, indeed, how visitors or keepers are able to use the enclosure area. For example, Wilson *et al.* (2003) were able to determine that visitors and keepers using a new giant panda exhibit at San Diego considered the changes to the enclosure favourable.
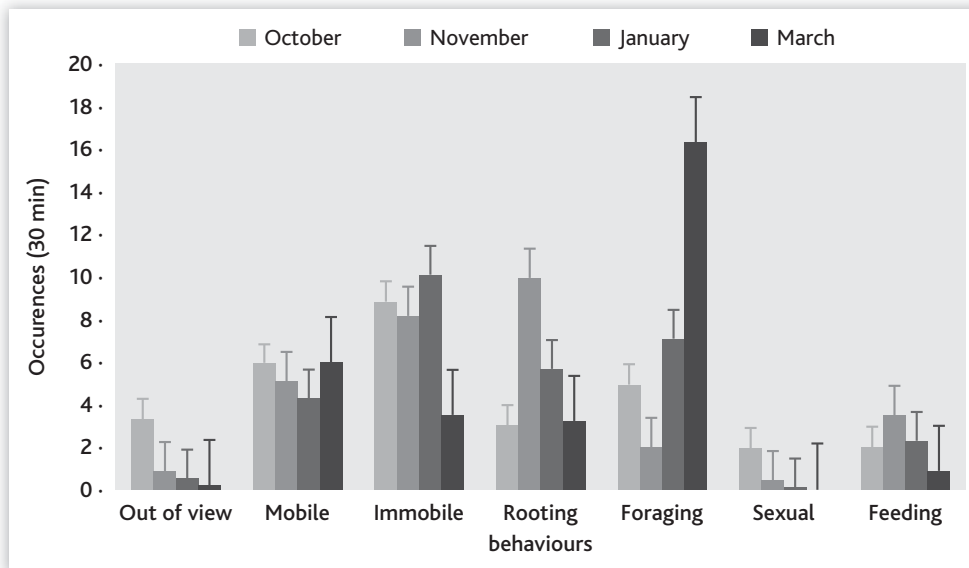
Figure 6.24 Enclosure use (the spread of participation index) by three red river hogs at Paignton Zoo Environmental Park in the first four months after they entered the new enclosure. In October, the hogs first entered the enclosure; in March, the hogs were fed using a scatter feed, which increased their use of the enclosure. (From Dayrell and Pullen 2003)

referred to by all zoos, because it is required that these recommendations are met in order to obtain a zoo licence (see **Chapter 3**). Also, it is a requirement of most captive management programmes, regardless of zoo association, to produce housing and husbandry guidelines. Yet these are surprisingly sparse given the number of animals in captivity: the International Species Information System (ISIS), which acts as a library for many of these documents has 292 husbandry manuals stored in their database (see **section 5.7.1**).

There are also some concerns about the quality of some of the guidelines that are available. From a rapid survey of guidelines produced worldwide, three out of nineteen were found to have some scientific basis for the housing and husbandry recommendations made, compared with scientific evidence in all veterinary sections in the same guidelines (Melfi *et al.* 2004a). It seems obvious that good housing and husbandry guidelines should be underpinned by evidence, essentially empirical data, which demonstrates why certain housing and husbandry principles should be employed. Therefore it appears that there is a need to encourage research investigating the impact of housing and husbandry, so that recommendations can be made based on evidence, and that those involved in captive management programmes should be encouraged to write housing and husbandry guidelines to facilitate zoos in providing the best possible conditions for their animals (see **Box 6.3**).

Box 6.3 EVIDENCE-BASED CAPTIVE ANIMAL MANAGEMENT

Many different types of information can be collected in a zoo about the animals in the collection, and we trust the reliability of some of this information, notably primary and objective information, more than others. However, when making decisions about the animals in our care we encounter a lot of information, and we don't want to simply ignore it because we weren't around when it was collected or it is subjective. So how do we proceed?

First and foremost, we can be aware of how to rate the reliability of information. We can consider that the reliability of information lies somewhere along a scale, from highly reliable to highly unreliable; information collected objectively during the course of an in-depth study (for example, a PhD) following a rigorous method of data collection (empirical) is likely to be highly reliable, whereas a story told in pub by someone who heard the story from someone else (anecdote) is probably worth considering with more caution (**Plate 6.1**)!!

In the scientific community, researchers publish the results of their studies in journals, to share their findings. Journals only want to publish studies which contain highly reliable information.

Therefore, prior to publication, other scientists (peers) read the study and they can decide to reject the study if they do not think that it is reliable. Once a study has passed this test, it is published in a peer-reviewed journal; this means that not only was the information gathered under very strict conditions, but also other scientists considered it to be reliable. Therefore the reliability of this information is considered to be very high.

But how reliable does information need to be, to inform a housing and husbandry decision? It makes sense that if we are presented with

Empirical study
        Peer-reviewed literature
        On site research
        Grey literature (non-peer-reviewed)
        Ad hoc observations
        Word of mouth
Anecdote
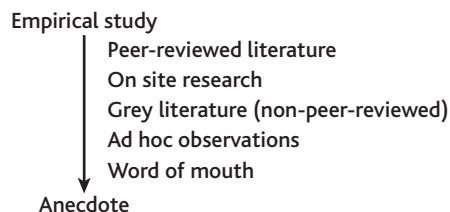
Figure 6.25 An illustration of how we can rate the reliability of different evidence from high (peer-reviewed) to anecdote (man down the pub). We use the following words interchangeably: evidence = information = data.

different types of information we choose to believe the information which is most reliable. But in the zoo community there is often a paucity of information, and so we might only have less reliable information available. Using less reliable information is not a problem; it just means that we need to be more cautious when using it.

In practice, if we were developing an environmental enrichment timetable, for example, we would gather as much information as possible about the enrichments we could use and determine which had been used previously with the target species and found to be successful. Enrichments which had been formally studied and published in peer-reviewed journals could be incorporated with little hesitation, whereas enrichment used by colleagues, which hadn't been studied or witnessed, would need to be introduced while keepers or other zoo professionals are present, and ideally the impact on the animals' behaviour monitored, so that we then had 'good reliable information' about whether the enrichment was successful.

So in summary, we can assess the reliability of different pieces of information, and accordingly have confidence in it or else consider it with caution.

Zoos generate a lot of information which results from daily operations, much of which is in the form of records (see **Chapter 5**). Incorporating this information into best practice could enhance the functioning of the zoo, for the animals and the overall operation (see **section 15.1**). Unfortunately, much of our housing and husbandry is informed by myth and tradition, rather than reliable data; which means that we might not be doing the best for the animals (Melfi 2009). For example, owing to keeper or visitor needs, traditional routines may have fed tawny frogmouths *Podargus strigoides* at 08.20 daily, which is inappropriate as this is a nocturnal animal. By applying a more evidence-based approach to zoo animal management we might find that feeding the frogmouths at a more appropriate time could increase the chance of breeding behaviour, or some other benefit. In summary, a common theme throughout this book, in fact one of the premises on which it is written, we need first to understand the principles (gather good evidence), so that informed decisions can be made, then we need to evaluate the consequences of our intervention, and so on … (**Fig 8.17** for a summary of enrichment planning and evaluation which follows an evidence-based approach).

Summary

• Enclosure design is usually a compromise between what is in the best interests of the needs of the three main stakeholders—that is, animals, keepers, and visitors—although the needs of other parties should also be considered.

• From initial enclosure design through to managing the animals, everything should be done to ensure that housing and husbandry stimulate the animals both physically and psychologically.

This can be more readily achieved by adopting an evidence-based approach.

• Housing and husbandry should also enable the keepers to maintain and promote good animal welfare.

• Housing and husbandry should provide an experience that is enjoyed by the visitors, who are hopefully able to learn something on their way around the zoo.

• An example of an enclosure in which all these measures have been incorporated is shown in **Fig. 6.26**.

Figure 6.26 If you have absorbed the contents of this chapter, you may be on your way to being able to design a world-class enclosure like that shown here for the Hamadryas baboon *Papio hamadryas* at Singapore Zoo, which has been faithfully modelled on their native Ethiopian mountains. (Photograph: Nor Sham/ Singapore Zoo)

Questions and topics for further discussion

1. Who are the three main stakeholders in zoo animal enclosure design and which other parties should also be considered?
2. What factors affect animals' needs in terms of their housing and husbandry?
3. What advantages and disadvantages are associated with naturalistic enclosures?
4. What methods might you use to stop an animal escaping?
5. Why is the management of social groups difficult?
6. Discuss, giving reasons to support your argument, whether enclosure size or complexity is more important.
7. Describe evidence-based captive animal management.
8. How would you evaluate the impact of a change in housing and husbandry on animal biology.

Further reading

Much of the material that you have been reading in this chapter has come from the experiences of people who work in the zoo world and a lot of it, where published, has been referred to appropriately in the chapter.

There are few books to which we can direct the reader specifically, although, as always, Kleiman *et al.*'s *Wild Mammals in Captivity: Principles and Techniques* (1996) and its successor the second edition (Kleiman *et al.* 2010) are fonts of information on the maintenance of mammals in zoos. For Australian mammals, we recommend Jackson (2010).

A number of journals—notably, *Applied Animal Behavioural Science*, *Zoo Biology*, *Animal Welfare*, *Aquarium Sciences*, and *Conservation*—publish papers of relevance to housing and husbandry. We can also mention the *International Zoo Yearbook*, which always has a number of case studies of housing and husbandry related experiences from various zoos.

Finally, it is worth reading the proceedings of the Zoo Design Conferences, which are available through the Whitley Wildlife Conservation Trust.

Websites and other resources

On numerous occasions in this chapter we have referred to the SSSMZP (Defra 2012a).

This is available to download and read in its entirety at **http://www.defra.gov.uk/publications/ 2012/09/11/standards-zoo-practice-pb13806/**

We should also direct you to the ZooLex website (**http://www.zoolex.org**) which is endorsed by the World Association of Zoos and Aquariums (WAZA) and provides an extensive zoo animal design bibliography, as well as numerous case studies about zoo exhibits constructed worldwide.

This chapter has been biased toward terrestrial enclosures, but there is an appendix on aquariums in the SSSMZP (Defra 2012a), and additional health and safety guidelines specific to managing aquariums have been produced by the HSE (2006). The need to oxygenate water, the complexity of the various filters used, and their availability, along with other useful information, can be found in standard textbooks dedicated to this subject, such as Spotte (1992), Moe (1993), Boness (1996), Hemdal (2006), and Adey and Loveland (2007). Chapters 23, 24, and 25 in the seventh edition of Fowler and Miller (2012) also provide a useful overview of the assessment of water quality in zoos and aquariums. See also **http://www.aalso.org/index.htm**

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.
http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Chapter 7
Animal welfare

All good **zoos** recognize that the animals in their care should have good welfare, regardless of the conservation, education, or research goals or missions that they aim to achieve. Animal welfare is commonly considered to be the subjective state of well-being of an individual, and is determined by both its physical and psychological condition.

Assessment of an animal's subjective state is very difficult and has until recently received little attention, and for the most part been the domain of anecdotal evidence. However, innovative and elegant research is now shedding some light into the world of animals' emotions, which is explored in this chapter. Because of difficulties inherent in studying animals' subjective states, much animal welfare research, and the evaluation of an animal's welfare state, has been largely based on objective but indirect measures of welfare.

Understanding and evaluating animals' needs, which, we assume, if satisfied lead to good welfare, has been pursued via four different approaches, from the perspective of their minds, bodies, and natures, and also by analogy. In this chapter, we will highlight some broad underlying animal welfare concepts and detail the approaches taken to study animal welfare states scientifically. We will review the biological and psychological processes which impact on the animal's welfare state, as well as the indices which can be used to measure this. Furthermore, circumstances that appear to significantly affect welfare state will be explored. Finally, we will also consider how zoos are able to meet the needs of the animals in their care and how they aim to provide the animals with good welfare.

The topics to be covered are as follows.

7.1   **What is 'animal welfare'?**
7.2   **Animal welfare science**
7.3   **What can affect zoo animal welfare?**
7.4   **Indices used to evaluate zoo animal welfare**
7.5   **Meeting the needs of zoo animals**

The accompanying boxes consider some related topics in a bit more detail, including some of the theoretical background that underpins this area (the stress response), methods that are used to assess biological function (non-invasive use of **cortisol**) and animal emotions, and topics that impinge on the subject of welfare (pain, deviations from normal). In addition, we will consider the utility of using longevity as a welfare indicator for zoo animals; which is highly controversial!

7.1 What is 'animal welfare'?

Animal welfare science is the study of an animal's quality of life, and more research has been undertaken on this within agriculture than in any of the other situations in which we keep animals. This has led to great advances in our understanding of the welfare of farm animals and has also provided us with general principles that are applicable to animals in other situations, such as the zoo. For this reason, much of the research that we quote in this chapter has come from the studies of agriculturally important animals.

We have to recognize that the welfare of animals does not change simply because we perceive it to be good or bad, or because we condone or deplore the use of animals in certain circumstances within our society. Animal welfare is the subjective state of an animal, which is independent of us and our societal views about welfare. However, the way in which we view welfare does greatly impact on the way in which we treat animals and therefore the conditions that we provide for them. Furthermore, Fraser (2008) illustrates how our cultural differences, in relation to our use of animals, have also moulded the questions we ask and our approach to studying animal welfare as a science (see **section 7.2**). We should also recognize that welfare is peculiar to an individual. Therefore welfare may differ between different animals when they are exposed to the same circumstances and, indeed, even the welfare of the same animal may vary over time.

7.1.1 It's all about the individual

Individuals, by definition, are different from one another, which means that they will experience the world differently and have different needs. There is variation in the extent to which even closely related individuals may develop disease, morphological abnormalities, and behavioural **pathologies**, and these may reflect underlying genetic differences. We have already considered how individual differences in factors such as sex, age, and social rank, and thus the needs of individuals, influence how we provide captive housing and husbandry (see **section 6.1.1**). In the next section, we will explore the impact on the animals' welfare of, firstly, those individual differences that can best be summarized as differences in personality, and secondly, the shared differences held by individuals of the same species.

Personality

'Personality' is an animal's consistent reaction to different environmental variables, resulting from a synthesis of the animal's genetic make-up and its past experience (see **Box 4.2**). Use of the term 'personality' is now widely accepted, though alternative terms, such as 'behavioural **phenotype**', 'suites of behavioural traits', 'behavioural syndromes', 'coping style', and 'temperament', are used in different scientific disciplines (see Wolf and Weissing 2012). Fig. 7.1.

Increasingly, data are emerging that demonstrate an association between reactions to **exogenous** and **endogenous stimuli** and differences in personality. For example, work undertaken by Dingemanse *et al.* (2010) demonstrated that differences in personality were associated with consistently different behavioural reactions to environmental factors along a gradient; i.e. as the environmental variable changed the animals' response to it changed consistently according to their personality type. This was shown in a variety of different species, including insects, fish, birds, and mammals (e.g. cheetah). Furthermore, there is a large body of evidence which describes different physiological reactions to stimuli between individuals, resulting, for example, in different levels of plasma cortisol levels; differential responses to stressors by individuals are sometimes termed coping styles (for a review see Stamps and Groothuis 2010). Personality differences between individuals are related to fitness benefits such as breeding success (Biro and Stamps 2008), but knowledge of an animal's

personality can also provide us with an insight into how it will perceive and react to factors in its environment, which can enable us to assess its welfare under different conditions. An association between personality differences and resilience or susceptibility to ill health has been demonstrated in humans, and this seems to hold for animals as well. For example, Cavigelli *et al.* (2006) demonstrated the degree of **neophobia** observed in mice could be linked to the onset and development of pathology, and the eventual death of the animal; this appeared to be due to underlying differences in neuroendocrine function between mice, which was itself linked with different temperaments. **Neophilic** animals, those that actively explored their environment, were more likely to die later than their neophobic siblings.[1]

Species differences

Within zoos, there are many different species of animals that are adapted to different environmental conditions and thus have different needs. Although, as we have seen, different individuals perceive information about their surroundings differently, nevertheless there are often physical characteristics that are shared by individuals of the same species and which may be different from those of other species. These characteristics can affect the animals' responses to **stimuli**.

A good example of this kind of species difference is hearing sensitivity. When Voipio *et al.* (2006) controlled for the difference in hearing sensitivity between rats and humans, he found that noise made during the hurried routine cleaning of stainless steel cages in a laboratory generated noise levels that exceeded 90 dB (weighted for the rat's sensitivity) and would not be considered a safe working environment for humans (e.g. HSE 2006). Minor changes to the husbandry routine, using polycarbonate cages in an unhurried

fashion, could make a significant reduction of 10–15 dB in the noise generated from this daily husbandry procedure. We know very little about noise levels in zoos and how they affect animal welfare (see **section 6.2.10**).

A second example of species differences concerns **stereotypies** (**Fig. 4.31**). We have already discussed these behaviours and looked at some examples from a range of species (see **section 4.4.3**). There is some evidence that the propensity to perform stereotypies is heritable in species as different as African striped mice *Rhabdomys pumilio* (Schwaibold and Pillay 2001) and mink *Mustela vison* (Jeppesen *et al.* 2004).

7.1.2 Changes in our views of welfare

People's perceptions of animal welfare vary according to factors such as the animal's role in society (whether it is considered useful or a nuisance), how familiar we are with it, how attractive we find it, and how rare it is (Appleby 1999). **Figure 7.2** illustrates how just one species, the rabbit *Oryctolagus cuniculus*, is viewed within our society, ranging from being denigrated as a **pest** to sharing our home as a pet. The lives of these rabbits will be very different depending on how we see their role within our society, but nevertheless they experience the world in the same way and thus will have very different levels of animal welfare, much of which is dependent on how they are treated by us—people. Many of the species held in zoos are charismatic, rare, and considered attractive, so most people 'like' them and therefore expect them to be maintained in conditions that will result in a very high level of welfare (Appleby 1999).

People have these different views of animal welfare because of differences in their personal attitudes, emotions, and factual knowledge. But it also appears to be the case that people within different societies often share common views about

---

[1] The suffixes *–philia* and *–phobia* are derived from ancient Greek and, added to words, specify an affinity or liking for, or an irrational fear or avoidance of, something, respectively. Thus, **neophilia** is an attraction to novel objects or new situations, whereas **neophobia** is an avoidance of them.

Figure 7.1 The way in which individual animals react to each other and to their environment can be affected by their personality. Studies of personality in non-human animals have concentrated largely on domestic animals, but some work has been done on exotic animals, such as the cheetah *Acinonyx jubatus* (Baker and Pullen, submitted). (Photograph: Paignton Zoo Environmental Park)

Figure 7.2 Our perceptions of animals affect the conditions that we impose upon them and the degree to which we are concerned about their welfare. The rabbit can be a family pet (a) or a laboratory animal, or a pest species (b). Which of these animals do you think would have the better welfare? (Photographs: (a) Courtney Mahony; (b) Rob Howarth, www.iStockphoto.com)

animal welfare, because these views are shaped by common and shared interests, including culture and religion (Boogaard *et al.* 2006; Doerfler and Peters 2006; Heleski and Zanella 2006; Signal and Taylor 2006). How we view an animal will impact directly on its welfare, because it will be treated differently as a consequence of our perceptions. This is achieved through two routes: firstly, the creation and enforcement of legislation, and, secondly, consumer pressure. Animal welfare legislation—which, in the UK, extends back to 1876—has changed continuously over the years in response to societal values (Kohn 1994) (see **Chapter 3** and **section 7.5.4**).

'Consumer pressure' describes the concept of how societal values influence an issue (in this case, animal welfare) when consumers follow through on their convictions by purchasing only products that they condone. This can be facilitated and directed by coverage in the mass media. Within the agricultural sector, this concept is termed the 'willingness to pay' principle; changes to farming systems that improve animal welfare cost money, so consumers can promote welfare by making informed purchases and paying more for animals farmed under 'improved' systems. Unfortunately, it appears that people's 'willingness to pay' is not always consistent with societal values, so the cheapest product can still remain popular even if 'societal values' would suggest that it should not be favoured. A survey conducted by Maria (2006) demonstrated that, while many people felt that improvements to farming methods were necessary, this did not influence which farmed products they purchased. In such situations, consumers are not, in fact, exerting pressure to improve conditions, but are supporting the continued use of 'suboptimal systems of farming'.

The impact of consumer pressure in zoos has not been studied systematically in the same way as it has in agriculture. Nevertheless, it does seem to have shaped certain animal housing and husbandry practices, as we have already discussed in terms of a bias by zoos towards meeting the needs of visitors when designing enclosures (**Fig. 7.3** and **Fig. 6.7**). It is also apparent in the avoidance of certain practices, such as **euthanasia**, as management tools, perhaps because, even though they may be the most appropriate action to ensure good welfare, they nevertheless gain negative coverage in the media. It is likely that consumer pressure on zoos is effective because they are heavily reliant on the money that visitors bring to the zoo.[2] Furthermore, it is unlikely that many zoo visitors consider their visit to be a necessity, compared with buying food or medication. So a decision to stop visiting zoos, on 'welfare grounds', would probably constitute a relatively small effort on the part of the visitor compared with regularly paying higher prices for animals farmed under 'welfare-friendly' conditions. Hence zoos seem eager to meet the needs of visitors and to avoid negative consumer pressure.

7.2 Animal welfare science

Science involves the use of standardized repeatable methodologies that give rise to objective data. Many researchers and practitioners in the field of animal welfare aim to follow scientific principles when attempting to understand animal welfare better, because the data collected this way are considered to have a high degree of validity and can therefore be believed. It also avoids simply relying on human perception of the animal's state in order to interpret its welfare (see **Box 6.3**). That is not to say that subjective assessments of welfare are of no value. Work by Wemelsfelder (2007) has pioneered the use of subjective measures to evaluate animals' quality of life. Using 'free choice profiling' or 'qualitative behavioural assessment', people observe animals (directly or indirectly on video) and use subjective terms to describe them and make assessments of their quality of life (e.g. pigs

---

[2] In the UK, for example, many zoos are charities, with no external funding.

Figure 7.3 Given that many zoo visitors are attracted to, and spend much of their visit to the zoo watching, large and charismatic species, it is not surprising that the lives of these species in zoos and the study of their welfare attracts more attention than that of other species. (Photographs: (a) and (b) Moscow Zoo; (c) Jeroen Stevens, Lisbon Zoo)

(Wemelsfelder *et al.* 2001); dairy buffalo *Bubalus bubalis* (Napolitano *et al.* 2012); kennelled dogs (Walker *et al.* 2012)). A similar method is often employed in the study of personality, which adopts either a more subjective or a more objective route of measurement; the former requires people familiar with the animals to rate them according to different personality traits, and the latter uses traditional methods of behavioural observation (e.g. Watters and Powell

2012). What is important when using subjective measures such as these is that steps are taken to ensure that they are reliable and valid, which is true for objectively collected data as well. Wemelsfelder (2007) points out that an animal's quality of life is dependent on its subjective state and so attempts to measure this state are needed.

Four common approaches have been used when considering what animals may need and thus what we should provide for them to ensure that they have good welfare:

- animal minds, by considering animals' subjective experiences, including emotions and the contentious issue of **consciousness**;
- animal bodies, by assessing the ability of animals to thrive and survive in their environment;
- animal natures, by considering the behaviours in wild animals as a template for good welfare (e.g. Fraser and Matthews 1997; Appleby 1999);
- ourselves and other animals, in which we draw analogies from ourselves about the needs and abilities of other animals (e.g. Sherwin 2001).

These approaches are not mutually exclusive and overlap considerably, but an awareness of them is useful when we later consider how factors in the zoo may affect welfare, and how and what indices we can use to evaluate welfare (**sections 7.3** and **7.4**).

7.2.1 Animal minds

Is the animal 'happy'? This seems to be an extremely appropriate question when considering animal welfare, because the emotions that an animal feels in response to stimuli underpin how it perceives those stimuli and thus whether its welfare is enhanced or compromised. Animal emotions are key to understanding and measuring animal welfare. **Box 7.1** explores the concept of pain, which is thought only to compromise welfare when the physiological reaction to

withdraw from a painful stimulus (nociception) is coupled with an aversive emotional sensation (Gregory 2004).

Relatively little research has been conducted on animal emotions or the functioning of animals' minds, although there has been recent interest and advances in this area which we will review later. But first, why has so little research been undertaken on animal emotion when it is central to our understanding and evaluation of animal welfare? There are several reasons why this is the case, but we will explore possibly the most prominent. Firstly, animals' minds, like our own, are private and may remain forever subjective. Inferences about animal minds can be made through the collection of suitable indices of behaviour and **cognition**, but, on the whole, this discipline does not lend itself to objective and empirical evaluation. As a consequence, many animal welfare scientists have preferred to collect data following the animal bodies' approach (**section 7.2.2**), which is seen to offer clear quantifiable units of measurement (Duncan and Fraser 1997). Secondly, animals' minds and emotions appear to be misunderstood (Midgley 1983; Wemelsfelder 1999), and so studies in this area are not as popular as they might be. This may be, in part, due to the convergence of different disciplines that all study animals' minds, but nevertheless use their own particular terms. Thus, biologists, sociologists, economists, psychologists, philosophers, and the mass media all have something to say about how animals feel and perceive the world, but use the language of their own discipline. Coupled with this, some of the terms may be used differently in the different disciplines, or in a vague way, or may be considered to be and thus used as synonyms. Terms associated with the study of animals' minds, and which often cause definitional problems, include 'affective' (to do with emotion), 'cognitive' (to do with knowledge and the processing of information), 'consciousness' (**self-awareness**), and **sentience** (to do with feeling). Finally, until relatively recently, the study of animal minds

Box 7.1 PAIN

> Pain in animals is an aversive sensory experience caused by actual or potential injury that elicits protective motor and vegetative reactions, results in learned avoidance behaviour, and may modify species specific behaviour, including social behaviour.
>
> (Zimmerman 1986)

As such, pain is considered to be an important part of the **learning** process in animals. It is likely that pain in animals, as in humans, is associated with suffering (reviewed by Rutherford 2002). Pain is thought to operate on both a physical and an emotional level. Specialized receptors (termed 'nociceptors') detect changes in heat ('thermoreceptors'), pressure ('mechanoreceptors'), and chemicals ('chemoreceptors') from noxious stimuli. The process of transporting the information from these receptors to the central nervous system (CNS), where it is integrated to promote a response, is illustrated in **Fig. 7.4** and is called 'nociception'. Nociception is essentially a reflexive neurological response to aversive stimuli, which does not necessarily involve perception of pain.

Whether animals actually perceive pain is a complex issue. Much of our knowledge about pain is derived from our human experience and understanding of the phenomenon. Flecknell and Molony (2003) pointed out that differences in pain perception between humans and animals should be borne in mind to ensure that some animal pain is not overlooked. Certainly, animals often show behavioural responses to aversive stimuli that we recognize as similar to our own responses to pain (reviewed by Weary *et al.* 2006); it also makes evolutionary sense for animals to feel pain, so that they reduce or avoid further damage to already injured parts of the body, providing time for recovery.

Pain perception can be divided into three different components according to its perceptual and behavioural effects, and these appear to be located in different areas of the brain (Price 2000):

(1) a sensory or physical component (or nociception), which leads to withdrawal and avoidance of the stimuli;

(2) immediate emotional consequences (acute pain);

(3) long-term emotional implications (chronic pain).
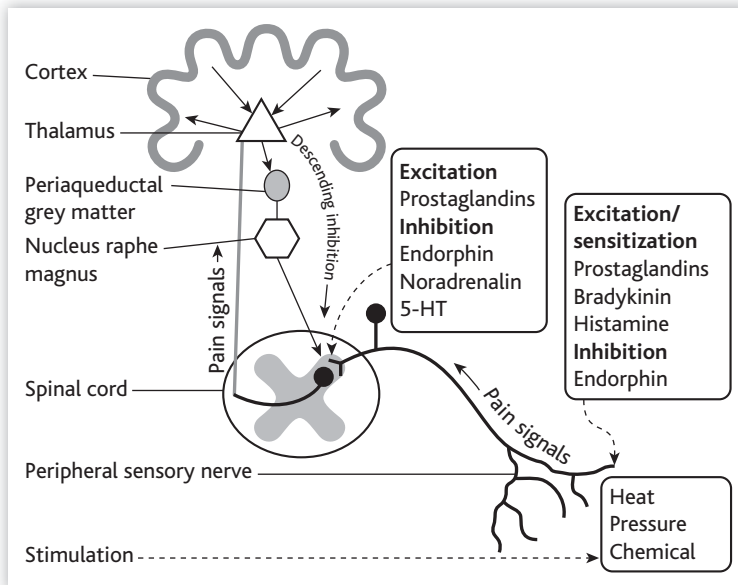
Figure 7.4 Information about noxious stimuli is detected via three different types of nociceptor: chemoreceptors, thermoreceptors, and mechanoreceptors. If any of these receptors is stimulated, information is sent to the central nervous system (CNS) via the sensory nerve fibres. The CNS integrates the information coming from the sensory nerves and initiates a response via motor nerve fibres. Information travels more quickly from mechanoreceptors than from other types of receptor, because their fibres are myelinated (they have a myelin sheath around the nerve fibres).

Pain is clearly of welfare concern in itself, but also because it may lead to additional problems, such as hunger, thirst, and social conflict, which occur when an animal experiences pain and is incapacitated. Although pain can be modified in a variety of ways in humans, '*by opiates, hypnosis, the administration of pharmacologically inert sugar pills, other emotions, and even other forms of stimulation, such as acupuncture*' (Carlson 2007), prevention is better than cure in both humans and animals. Unfortunately, it is inevitable that all animals in zoos will experience pain at some time or another because of illness, injury from the enclosure or a cage-mate, transportation, or routine catch-ups. As mentioned previously, experiencing pain can have learning benefits, so we shouldn't be aiming to maintain animals completely free of pain; instead it is essential that the potential for pain is reduced and that, when it occurs, everything is done to make the animal comfortable.

Of course, this requires that pain can be identified, which can be achieved in three ways by measuring general body functioning, physiological responses, and behaviour (Weary *et al.* 2006); see Gregory (2004) for some general observed behaviours that have been associated with pain perception in animals.

Many species express different behaviours as a result of pain that can be affected by their age and sex (Flecknell and Waterman-Pearson 2000). Added to this, many species kept in zoos have evolved to hide any signs of pain, because showing these would make them vulnerable to predation or social pressures. One clear method

of assessing whether pain is present is to administer **analgesic drugs**; if indicators of pain stop, then pain was present and has now been alleviated.

The capacity for different taxa to experience pain is an area of scientific exploration, although most speculation about this is directed toward non-mammalian and bird taxa. In these studies, a distinction is made between those species/taxa which are shown to display nociception and those which are considered to feel pain. Elwood *et al.* (2009) suggested critieria which could indicate the potential to experience pain; these included having a suitable nervous system and sensory receptors, displaying physiological changes and/or protective motor reactions (behaviour) to noxious stimuli, and showing avoidance learning. For example, Sneddon (2003) demonstrated that fish can feel pain. Rainbow trout *Oncorhynchus mykiss* were injected with a noxious substance (0.1 ml acetic acid) in their lips, after which they were observed to rock from side to side and rub their lips into the gravel flooring substrate of their tank. When the trout were administered a morphine injection intramuscularly (morphine sulphate 0.3 g/1 ml sterile saline), as well as the noxious substance, the above behaviours were performed at significantly reduced levels and thus were interpreted to be pain-related behaviour. Subsquently, other studies have supported the fact that fish feel pain (e.g. Braithwaite and Huntingford 2004; Chandroo *et al.* 2004; Sneddon 2009). There are also data which suggest that invertebrates can also feel pain.

was not considered to be scientifically valid. The attribution of emotion to non-human animals was a concept that developed in the eighteenth century, during the Enlightenment, and which

has been a contentious issue ever since (Duncan 2006). The concept went out of favour in the twentieth century, largely due to the influence of Behaviourism.[3] Watson (1928), one of the

[3] **Behaviourism** was a scientific discipline that viewed mental events as unknowable and, in its most extreme form, denied that they existed. This led behaviourists to study only observable behaviour, so that their view of animals was effectively of automata whose behaviour was shaped by stimuli through a process of **operant conditioning**.

founders of Behaviourism, neatly sums up its position:

> The behaviourist sweeps aside all medieval conceptions. He drops from his scientific vocabulary all subjective terms such as sensation, perception, image, desire and even thinking and emotion.

Such was the influence of this approach that animals were regarded as automata, or 'black boxes', whose most complex behaviours were considered to be the result of a series of stimuli–response processes, and were neither influenced by 'consideration' nor affected by 'emotion' (Skinner 1938). Griffin (1992) did a great deal to bring the issue of animal sentience back into the realm of scientific discussion, using extensive reviews of animal behaviour as evidence for his strongly held belief that the highly complex behaviours observed in many species indicated they were, indeed, sentient. More recently, Burghardt (1995) has gone so far as to suggest that Tinbergen's (1963) 'four aims of ethology' (see **Box 4.1**) should be expanded to include the exploration of animals' subjective states.

Despite a general reluctance to explore animal emotions, Panksepp (2011) provides compelling objective data that '*there is now abundant experimental evidence indicating that all mammals have negatively and positively-valenced[4] emotional networks concentrated in homologous brain regions that mediate affective experiences when animals are emotionally aroused*'. Using localized electrical stimulation to the appropriate site in the brain, Panksepp (2011) notes that seven 'powerful unconditioned emotional responses' will result—those of seeking, rage, fear, lust, care, panic/grief, and play. Using these emotional states as a road map, Morris *et al.* (2011) review further the emotional lives of captive animals, and suggest that captive animals will be highly motivated to perform behaviours resulting from these emotions. As such, they suggest that environmental enrichment

should be designed to better enable captive animals to perform these behaviours, which will as a consequence promote good animal welfare. One of the examples they suggest is the provision of a secluded area for nesting hens, which they consider will satisfy the birds need to hide, which itself will be driven by the emotional state of fear.

As well as the neurological basis of emotions, much is being learnt from adopting a behavioural experimental approach. Meagher and Mason (2012) operationally defined terms used to describe three different negative emotional states: boredom, a situation where animals are motivated to seek stimulation; apathy, when animals' motivation and participation in activities decreases, demonstrated by decreased motivation to obtain or interact with stimuli; and depression (more specifically anhedonia), considered to be a reduced capacity to experience pleasure, indicated by a reduced intake of rewards. Adopting a systematic approach, empirical data were collected on caged mink, which Meagher and Mason (2012) interpreted to suggest that the mink were experiencing neither apathy nor depression, but that they were bored, indicated by long periods spent lying still but awake; when stimuli were presented the mink showed a heightened degree of investigation. Another approach being employed to study animal emotion is cognitive bias (see **section 7.4.6**).

The issue of sentience is still controversial, but even some of those who are unhappy with attributing sentience to animals suggest that we should give them the benefit of the doubt, just in case (Barnard and Hurst 1996)—a concept that underlies the fourth approach to the study of animals described in this chapter, that of welfare by analogy.

And this brings us back full circle to the eighteenth-century Enlightenment and the sentiments of philosopher Jeremy Bentham who, in 1789, is famously quoted as declaring: '*The question is not, "Can they reason?" nor, "Can they talk?" but, "Can they suffer?"* '

---

[4] Valence is a term used to describe and categorize whether an emotion is positive or negative (e.g. joy versus anger) and is more generally considered to be the outcome of a positive or negative event or situation.

7.2.2 Animal bodies

How well does the animal cope in its environment? The 'animal bodies' approach to welfare considers the physical well-being of animals and is based on the concept of **homeostasis**, whereby a combination of biological processes serves to maintain the animal's body in a stable state (or a state of balance) so that it can carry out necessary survival functions. Animal welfare is considered to be compromised and the animal unable to cope if either homeostasis cannot be achieved, or the physiological and/or behavioural responses that are implemented to achieve homeostasis put undue pressure on the animal and, as a consequence, it is no longer able to 'cope' effectively within its environment. Therefore it is important to note that the reaction of the animal to stimuli is not, of itself, evidence of welfare being compromised, if the animal is able to react appropriately and still continue functioning with ease. Welfare is only compromised if the stimuli inhibit the appropriate functioning of the animal.

Alternatively, it has been proposed that rather than measuring animal welfare in terms of an animal's ability to maintain homeostasis, the extent to which an animal can successfully deviate from homeostasis when challenged by stimuli, termed allostasis,[5] may be more meaningful (Korte *et al.* 2007). Allostasis, has been described to '… *involve whole brain and body rather than simply local feedback'* (Sterling and Eyer 1988). As such, it

[5] Allostasis means stability through change.

encapsulates a more holistic approach to biological function (Schulkin 2003). Furthermore, in a zoo context, where genetic diversity is maintained in animal populations to allow future plasticity, it makes sense to also maintain animals with the capacity to change behaviourally and physiologically. Studies of fish welfare have largely adopted the concept of allostasis (see reviews by Schreck 2010; Prunet *et al.* 2012).

The animal's reactions to stimuli, and subsequent functioning, can be measured systematically and quantitatively, and, as such, a variety of measures can be collected to study the ease, or otherwise, with which an animal is able to function in its environment. Furthermore, conditions can be experimentally manipulated to investigate how they affect welfare.

This approach is based on the stress concept, which was initiated by Selye (1973) and outlines how an animal's response to exogenous and endogenous stimuli (termed stressors) might be interpreted (see **Box 7.2**). The stress concept recognizes that the type of stressor, stress response, and individual differences affect animal welfare (Ewbank 1985). The physiological process that underlies the animal's reaction to the stressor is mediated by the hypothalamus, pituitary, and adrenal cortex—known collectively as the **hypothalamo-pituitary-adrenal (HPA) axis**— which is illustrated in **Fig. 7.5**, in which you can see that stimulation of the pituitary by a stressor leads to the secretion of adrenocorticotropic hormone (ACTH), which, in turn, stimulates the adrenal cortex to secrete **corticosteroids**,

Box 7.2 STRESS

There is a stable state at which the body can function efficiently and deviations from this reduce the animal's ability to function. Endogenous (within the body) and exogenous (outside the body) stimuli lead to deviations from this stable state and an animal's body is considered to be under stress at this time. Stress stimulates

various biological regulatory mechanisms to kick in, the expression of which brings the body back to a stable state; this whole process is termed homeostasis, or the homeostatic control system, whereby the body is maintained in a stable state.

The biological process of stress is one that animals (including ourselves) experience much of

the time and, in most circumstances, it goes unnoticed because appropriate homeostatic regulation brings the body back to a stable state. This means that *stress does not necessarily indicate poor welfare*, and hence some have suggested that the term stress be restricted for use only when pathology occurs, which implies negative welfare (Fraser *et al.* 1975). Therefore physiological and behavioural measures indicative of stress are not necessarily indicative of poor welfare.

Selye (1973) considered that stressors led to a stress response that was stereotyped (always the same), non-specific (occurs regardless of stressor type), and triphasic (made up of three sequential phases: alarm response; resistance; exhaustion) referred to as the 'general adaptation syndrome' (GAS). The alarm response is induced by the sympathetic nervous system[6] and responsible for the 'fight or flight' response, when the animal is physiologically prepared for muscular exertion as blood supplies are rerouted to supply priority organs, and energy is metabolized and directed towards muscles, away from vital organs. If the stressor continues, the animal will need to make adaptations to the way it functions, which may be seen as changes in behaviour or physiological processes. Resistance is characterized by overproduction of glucocorticoids and a decrease in lymphocyte number, which characterizes impaired immune function and makes the animal susceptible to disease. If the animal is unable to adapt adequately, or if the stressor is extreme, the animal may enter the final exhaustion phase, and it is at this point that its biological functioning is compromised and it can no longer 'cope' in its environment. If the animal's biological functioning is severely compromised, it will die.

The duration and intensity of stressors, and how they are perceived by the animal, will determine whether an animal moves through all three phases of the stress response or stops at one of them (Dantzer 1994). **Table 7.1** illustrates how different stressors might affect the animal, and the point at which they might be considered aversive and compromise animal welfare; if a stressor reduces the animal's ability to function in its environment, animal welfare can be considered to be compromised.

Type of stress (intensity)*	Phase (according to GAS)**	Animal's state***	Biological observations
Innocuous	Alarm (initial)	Eustress	Short-term changes, no compromise to functioning
Aversive	Resistance (continued)	Overstressed	Long-term changes, ability to function impaired
Noxious	Exhaustion (long-term)	Distressed	Unable to adapt to stressor and so damage is incurred
Extreme			Death is likely

Table 7.1 The impact of stressors on the biological function of animals

*After Broom and Johnson (1993)

**After Selye (1973)

***After Ewbank (1985).

Note: The impact of stressors on the biological function of animals is determined by their type, duration, and intensity. The table shows how the different phases of the general adaptation syndrome (GAS) are related to other means of defining stress, i.e. whether the stress is innocuous—termed 'eustress' by Ewbank (1985).

[6] **The sympathetic nervous system** is a part of the nervous system, the effects of which include increasing activity, speeding up the heart and circulation, and slowing down digestive processes.
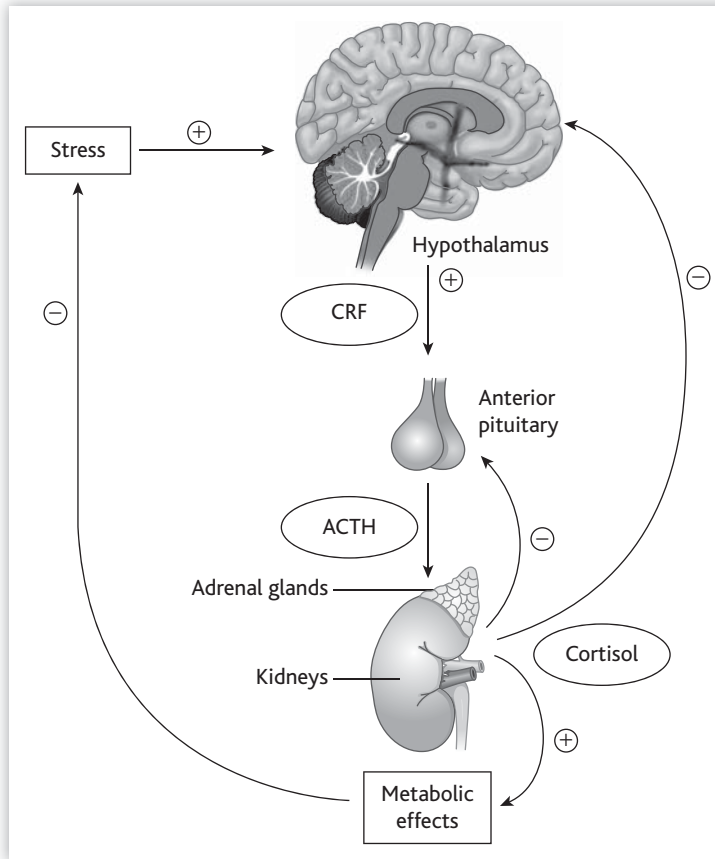
Figure 7.5 The stress response is mediated by the hypothalamic–pituitary–adrenal (HPA) axis. The hypothalamus instructs the anterior pituitary to secrete hormones which, in turn, exert an effect on the outer part of the adrenal glands (the adrenal cortex); this, in turn, secretes glucocorticoids. Nerve pathways from the hypothalamus affect the inner part of the adrenal cortex (the medulla) which, in response, secretes catecholamine hormones (adrenaline and noradrenaline). Note the similarities to the HPG axis (**Fig. 9.5**).

namely cortisol and its metabolites—hence their pivotal role as indicators used to measure stress (this is further explored in **Box 7.3**). As we have already suggested, the different approaches to animal welfare (minds, bodies, natures, and analogy) are not mutually exclusive. Studies which have investigated a more integrated approach to animal welfare can tell us a great deal. For example, studies which have shown a disparity in HPA axis response to aversive stressors support the suggestion that an animal's emotional perception of a stressor can determine its physiological response, i.e. whether it is negative or neutral or positive (Veissier and Boissy 2007; Schreck 2010).

7.2.3 Animal natures

The third approach to animal welfare considers that wild **conspecifics** are examples of animals with good welfare and can be used as a template by which the welfare of other animals is judged. It follows that, if an animal has evolved as a consequence of performing certain functions, then the inhibition of these will reduce welfare; this approach most commonly adopts behaviour as a welfare index, and as a consequence assesses this in captive and wild animals (see **sections 4.5** and **8.3.1**). Zoo animal welfare is believed to be compromised as a consequence of **behavioural restriction**, which is considered to result from situations in which animals are not able to express their full repertoire of behaviours (see **section 7.3.2**).

There are some problems in adopting the animal natures approach. As Barnard and Hurst (1996) point out, the welfare of many wild animals may itself be considered poor. Indeed, some behavioural patterns, such as aggression and flight responses, occur in the wild when animals are under a high degree of stress (Spinka 2006).

So, in fact, only a selection of the behaviours observed in the wild, which are thought appropriate for captive animals to display, are usually considered in any comparison of wild and captive animals. There are also some methodological difficulties in undertaking wild–captive comparisons (Veasey *et al.* 1996a, 1996b) (see **section 4.5.1** for more on this).

In some situations, there may be a deleterious mismatch between the environmental pressures that have shaped an animal in its native habitat and those that it faces in captivity. Historical records show that breeding and survival in zoos have improved in recent years (Kitchener and Macdonald 2004), which may be due to improvements in husbandry and housing (**Fig. 7.6**) (see **Chapter 6**) or to adaptation to captivity. Thus the natures of animals in captivity are likely to be different from their wild conspecifics or ancestors. Sometimes the disparity between wild and captive animal behaviour is measured as a function of behavioural restriction (see **section 7.3.2**); the net welfare impact of adapting to captivity is considered in **section 7.3.3**.

7.2.4 Welfare by analogy

Arguments of analogy are based on the principle that homologous physiological and behavioural processes between humans and other animals have analogous functions. In the context of animal welfare, we (humans) share many biological structures with other animals and we can experience different welfare states; thus the same must be true of animals. This approach is not new. We have already mentioned Jeremy Bentham (1823) who was the first to use the argument of analogy. Interestingly, he used this argument to suggest that different people could also experience the world similarly, namely slaves and their owners. Contemporary animal rights philosophers, such as Peter Singer and Tom Regan, continue to use similar arguments, explicitly suggesting that by virtue of shared characteristics, humans and animals should be considered and treated equally within society (Singer 1975; 2009; Regan 1983).

For the animal kingdom at large (which is very large) there is little scientific evidence to support the use of welfare by analogy, though it is still widely accepted within the scientific community (Dol *et al.* 1999). Furthermore, the use of welfare by analogy is not even considered controversial for many animals we consider similar to ourselves (many mammals), especially those we're closely related to. However, when similar biological processes are discovered or reported to exist in taxa which are only distantly related to ourselves, namely invertebrates, the process of welfare by analogy becomes more debatable (e.g. cockroaches, flies, and slugs (Sherwin 2001); crustaceans and molluscs (Elwood 2011; Mason 2011)).

When following this approach, however, it is necessary to be ever cognizant of the complexity with which many different species will interact with and perceive the world so that we do not underestimate the faculties of these animals because they appear similar to ourselves.

7.2.5 Integration

Although these four approaches to animal welfare have been described separately here, they should not be used alone and, indeed, relying upon only one approach has its limitations. Ironically, despite the study of animal bodies being the approach that dominates the field of animal welfare, most would agree that really a knowledge of animal minds is essential to understanding animal welfare. Rushen (2003) suggests that, without including an animal's subjective experiences alongside measures of physiological and behavioural responses to stimuli, the meaning of animal welfare is lost. Duncan (1993) supports this view, declaring that '*neither health, nor lack of stress nor fitness is necessary and/or sufficient to conclude that an animal has good welfare. Welfare is dependent on what animals feel*'.

Furthermore, an individual's emotional perceptions of the stressor will affect how the stress response impacts upon its welfare (Dantzer 1994). For example, the physical exertion necessary when either chasing (if a predator) or being chased

Figure 7.6 Advances in the health care available to exotic animals in zoos, as well as a better understanding of animals' nutritional requirements, are largely responsible for the decline in mortality rates seen in zoos. There is more about this in **Chapter 11** on 'Health'. (Photograph: Chris Stevens, Werribee Open Range Zoo, Victoria)

(if the prey) is extreme and is an example of a high-intensity short-duration stressor, but we can imagine that the emotional perception of the stressor will be viewed rather differently by the animal being chased than it is by the animal doing the chasing.

The need to include the individual's perception of the stressor is mentioned throughout this section but, unfortunately, measuring this variable is difficult.

7.3 What can affect zoo animal welfare?

Previously the study of animal welfare has been dominated by research which has investigated animals with poor animal welfare; considering what indices constitute poor welfare, what factors lead to the development of poor welfare, and what are the ramifications for animals which experience poor welfare. By contrast, the study of good animal welfare is a relatively unexplored, but research in this area is likely to yield more constructive and informative data, highlighting best practice rather than what should be avoided (Melfi 2009). What information exists about good welfare in zoo animals is incorporated in this chapter, namely pioneering research exploring positive welfare indices. More broadly, within this book, steps taken to meet the needs of animals to ensure good welfare are summarized in **section 7.5** and **Chapter 6**, which considers the housing and husbandry requirements of zoo animals. This section will

focus on **environmental challenge** and behavioural restriction, two areas which have been identified as significant factors which compromise the welfare of animals.

The management of animals in zoos presents additional challenges to welfare that are less of an issue in farm and laboratory animals, such as the steps undertaken for conservation and animal management programmes (for example, transport and introductions), and factors associated with exhibiting animals (for example, human–animal interactions and housing conditions). All of these factors might present environmental challenge or behavioural restriction, or result in adaptation to captivity, although the hope is to reduce this (see **section 7.5.2**).

7.3.1 Environmental challenge

The term 'environmental challenge' is used to denote the presence or absence of properties within the environment that may act to overstimulate or understimulate the animal. Morgan and Tromborg (2007) considered that zoo animals were '*confronted by a wide range of potentially provocative environmental challenges*' peculiar to living in captivity. These included artificial lighting, exposure to loud or aversive sound and arousing odours, and reduced retreat space. Whether in captivity or in their native habitat, animals have, of course, evolved to adapt to environmental challenges, including such things as changes in temperature, finding food, orienting themselves within their home range, and living in a complex social system. Given that many zoos maintain animals from all around the world and also transport them worldwide as part of **captive management programmes**, zoo animals are likely to experience, at the very least, a climate, day-length, and seasonal variation that is foreign to them. (This is reviewed in more detail in **Chapter 6** on 'Housing and husbandry'.)

Many of the issues associated with environmental challenge overlap, but, for simplicity, we will review them in terms of two factors: a lack of control or predictability, and novelty versus disturbance.

A lack of control or predictability

Frustration can develop—and thus welfare becomes compromised—in animals that lose control within their environment, or when events in their lives are not predictable. This is just as true for positive events in the animal's environment, such as the provision of food, as it is for aversive events, such as being caught up for a health check. Control and predictability are inextricably linked because control can be gained in a predictable environment or, from the other perspective, control can make the environment predictable (Bassett and Buchanan-Smith 2007).

An animal achieves control when its behaviour appears to determine the occurrence of an event or situation (Overmier *et al.* 1980). In a series of experiments on laboratory rats that had no control and could not predict the occurrence of an electric shock, the rats developed 'stress-related' symptoms including high corticosteroid plasma levels, stomach wall lesions, and compromised immune systems (Wiepkema and Koolhaas 1993). Rats that could predict the shock, because of a light that came on to precede it, or could control it by turning a wheel that interrupted or stopped the shock developed no more stress-related symptoms than 'control' animals who did not receive a shock at all (**Fig. 7.7**).

Bassett and Buchanan-Smith (2007) distinguish two different kinds of predictability:

(1) temporal predictability, which describes whether an event is provided at a fixed time (and thus is predictable), or at different times (so is unpredictable);

(2) signalled predictability, which is when a signal precedes an event and thus makes it predictable; the reliability of the signal may vary and thus change the reliability of the signal to predict the event.

There is a lot of contradiction in the published literature about the welfare implications of predictability in animal routines, although there is good evidence that animal welfare is improved
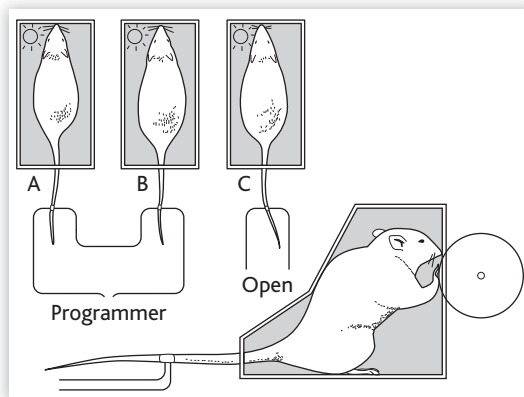
Figure 7.7 Rats housed in identical laboratory cages were positioned so that their tails were left protruding out of the cage. A weak electric shock was applied to the tails of the rats in boxes A and B; rats in box C were control animals and did not receive a shock. The rats in box A saw a light come on just prior to the electric shock, which provided a signal of the shock's imminent arrival, whereas rats in box B saw the light come on at random intervals so that there was no association between the light and the shock. The rats that had a signal (the light) prior to the shock showed a decreased response to the electric shock compared with those rats that were unable to predict its arrival. In a later experiment, rats in box A were able to prevent or interrupt the electric shock by turning a wheel at the front of the box when they observed the light. (From Wiepkema and Koolhaas 1993)

with signalled predictability, regardless of whether the event being signalled is negative or positive. The study on rats that we have just described (Wiepkema and Koolhaas 1993) supports this interpretation, because knowledge of the onset of an aversive event (an electric shock) reduced stress-related symptoms in the animals. In another study, it was found that **enrichment** had a significantly greater impact on piglets (measured as increased play and decreased aggression) when a signal preceded its presentation (Dudink *et al.* 2006). On the other hand, predictability within feeding regimes for some zoo-housed species appears to be detrimental to their welfare and has been associated with stereotypies (Carlstead 1998).

Challenge

Wemelsfelder and Birke (1997) suggested that animals in captivity were usually understimulated compared with their wild conspecifics, because their ability to explore and experience novelty was reduced. A lack of challenge is thought to have negative implications for animal welfare, leading to the development of apathy, boredom, and behavioural abnormalities (Stevenson 1983). In fact, the early development of enrichment aimed to counter this problem and was based on providing novelty to stimulate exploratory behaviours in animals (see **section 8.6.2**). However, enrichments that are based on novelty have a very short useful shelf life; once the animals are familiar with the items, they lose their novelty and no longer stimulate exploration. Thus the provision of environmental enrichment which is focused on challenge, rather than the provision of novelty *per se*, has far-reaching positive ramifications (Meehan and Mench 2007).

There might be circumstances where a challenge might not be appropriate; for example, novelty might be perceived negatively by the animal that is neophobic. Anecdotally, it seems that if animals have the means (both physical and psychological, as well as within their physical environment) to meet the challenge, there are long-term benefits for them. However, when animals do not have the means to meet a challenge in their environment, they are more likely to become frustrated which can lead to poor welfare. In one of the few studies where challenge has been quantified, Chamove and Moodie (1990) flew silhouettes of birds of prey over cages that housed cotton-top tamarins *Saguinus oedipus* in order to stimulate '*brief intense* [states of] *arousal*'. This, of course, mimics the sort of environmental challenge posed by real predators that the tamarins might experience in the wild. As a result, the tamarins showed fewer **abnormal behaviours** and more social behaviours, and the authors concluded that the arousal the model had induced was beneficial. Wiepkema and Koolhaas (1993) also thought that short periods of disturbance might stimulate captive animals because they promoted vigilance. There are more examples of situations where cognitive challenges have

been provided, and all appear to promote welfare (e.g. Clark 2011b).

Despite this, providing challenge has been associated with negative connotations of intentionally causing stress or frustration to animals in a captive environment, and so has been highly controversial (e.g. Roush *et al.* 1992). In some situations, this means that the sorts of feeding schedule that the animals would experience in the wild cannot be mimicked in captivity—for example, the provision of live prey (see **section 12.3.1**) or stopping food provision during hibernation). We are, of course, largely ignorant of how animals perceive negative events in their environment. We might, for example, expect veterinary procedures to be the most fearful events that a zoo animal encounters, and yet Langkilde and Shine (2006) found that moving yellow-bellied water skinks *Eulamprus heatwolei* to an unfamiliar enclosure raised their cortisol levels significantly higher than did **invasive procedures** such as toe-clipping, blood sampling, and microchip insertion (**Fig. 7.8**).

Fearfulness, then, may be caused by the presence of novelty or the absence of familiarity (as in the skink example). Neophobia is generally a sensible innate precaution to potentially dangerous environmental conditions or objects. For example, wild birds have been observed to avoid eating novel prey items because they may be poisonous, and rats are notoriously wary of unfamiliar foods.[7] Unfortunately, some husbandry procedures in zoos may inadvertently induce neophobia. For example, species that are highly reliant on odour as their major route of communication spend a great deal of time scent marking and this conveys valuable information about themselves to other animals. Presumably, it also makes the area in which they live more familiar to them. But the routine use of disinfectants and detergents to remove dirt, and thus reduce the risk of disease transmission, can also remove any olfactory
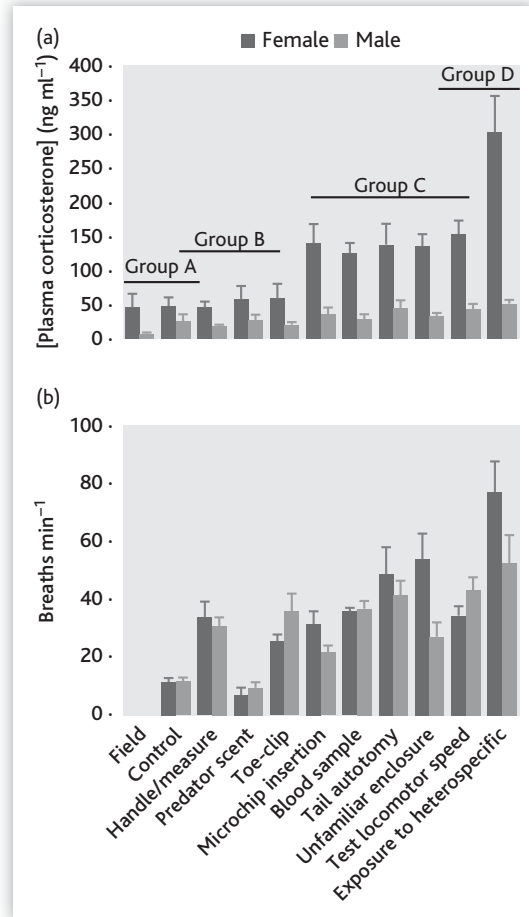
Figure 7.8 The stress response of twenty (ten males and ten females) yellow-bellied water skinks *Eulamprus heatwolei* was measured when they were exposed to different routine husbandry procedures: (a) Plasma cortisol levels (a measure of the stress response) taken 1 hour after an event; (b) the animals' respiration rates. There were significant differences in plasma cortisol responses for husbandry procedures A, B, C, and D. The greatest elevation in cortisol occurred when the lizards were exposed to a heterospecific (a lizard from another species). (From Langkilde and Shine 2006)

information laid down by the animal inhabitants, thus reducing the familiarity of the enclosure and potentially compromising the well-being of the animals (McCann *et al.* 2007).

---

[7] This wariness about novel foods probably explains the evolution of **aposematism**—that is, the use of warning colours or other conspicuous stimuli to advertise distastefulness or toxicity, as in ladybirds, for example.

There are other environmental challenges in the zoo environment, and these can include factors which we are aware of but perhaps do not notice, and also some (such as the olfactory signals just mentioned) that we may not be able to perceive. Noise from visitors and construction are both quite obvious disturbances through which zoos animals have to live (see **section 13.3.2**).

There are other, less obvious, factors than noise that can have an impact on animals. As an example, the flicker emitted from low-level fluorescent lights affects the mate-choice behaviour of European starlings *Sturnus vulgaris* (Evans *et al.* 2006); we have little idea how stimuli such as this affect most of the animals housed in zoos.

Figure 7.9 The use of chaining in elephant husbandry routines has decreased markedly in recent times in zoos. This practice is still employed on occasion, however, when the behaviour of the elephant may be unpredictable and when keepers are operating at close quarters—for example, when a female is giving birth, as seen here. (Photograph: anonymous)

7.3.2 Behavioural restriction

Dawkins (1988) asserted that behavioural restriction, the inability of animals to perform natural behaviours, caused them suffering, and underpins the 'natures' approach to animal welfare science. As an advocate of this approach, Rollin (1992) suggested that certain behaviours were of inherent welfare benefit to animals—a view that is often summed up as, '*birds gotta fly, and fish gotta swim*' (**Plate 7.1**).

So what can stop captive animals from expressing their full behavioural repertoire? In general, this can happen because of the direct or indirect impacts of housing and husbandry. Extreme examples are the use of wing-management techniques to prevent flying in birds (see **section 6.3.4**), physical restraint, or the use of contraceptives to prevent breeding. Physical restraint is usually a temporary measure and can occur when an animal has been caught for a health check, or for some routine activity within the husbandry regime. For example, a traditional method of housing elephants involves **chaining** (or **picketing**) (**Fig. 7.9**), whereby one front and the diagonal back leg are chained; the elephant is able to move approximately one step forward and one step back. Circus elephants

that had previously been chained in this way showed a significant reduction in the level of stereotypies that they displayed when they were provided with pens (paddocks) instead (Friend and Parker 1999).

Elephant chaining is an extreme example, but there are less obvious aspects of housing and husbandry that can also cause behavioural restriction, because they do not provide the opportunity for the animal to express some of its behaviours. For example, **flight distances**, which enable animals to get to a 'safe distance' from a stressor, may be severely shortened in enclosures that are too small. When animals in a **petting zoo** were able to retreat fully from visitors, their expression of undesirable behaviours was reduced (Anderson *et al.* 2002). Restrictions placed on the expression, duration, and diversity of feeding and foraging behaviours are considered to be a principal cause of the development of abnormal behaviours in captive animals (Rushen and Depassillé 1992) (see **section 4.4**).

It does appear to be the case that benefits are associated with the ability to express natural behaviours and, conversely, that deleterious effects occur when they cannot be performed.

Possible reasons why natural behavioural expression should be facilitated include the following.

1. Animals have evolved over many years to perform these behaviours and thus are highly motivated to express them, so they will experience frustration if the behaviours are inhibited (Stolba and Wood-Gush 1984; Shepherdson *et al.* 1993; Lutz and Novak 1995).

2. The performance of these behaviours is associated with positive affective experiences and long-term benefits such as enhanced adaptation to environmental stressors (Spinka 2006).

3. A 'void' will be created in their absence and 'abnormal' behaviours will develop in their place (Anderson and Chamove 1984; Chamove 1988), but it has also been argued that it is just as likely that behaviours of a negligible or beneficial nature could be performed instead (Reinhardt and Roberts 1997).

4. Animals will forgo cognitive stimulation if they are unable to express natural behaviours (Reinhardt and Roberts 1997).

5. Behavioural restriction indicates that environmental challenges of captivity have affected the animal and suggests that the animal has not been able to adapt to those challenges (Hutchings *et al.* 1978; Redshaw and Mallinson 1991).

It should be noted that these explanations are not mutually exclusive and that some of them may only partially explain what is happening to the animals.

7.3.3 Adaptation to captivity

When animals are in captivity, it is inevitable that successive generations will become adapted to the new environmental pressures in the zoo and thus adapt to life in captivity (Frankham *et al.* 1986). Through this process, the nature of zoo animals can change, indirectly and slowly, and is continuing to change. Animals that thrive and breed well in zoos pass on their genes to the next generation. If this process is permitted to carry on, disproportionately more 'adapted' animals will contribute to the next generation compared with those that do not adapt. As might be expected, the impact of this process grows with each subsequent generation. For example, in a longitudinal study of red jungle fowl *Gallus gallus*, anti-predator behaviour was observed to decline over four successive generations in captivity (Håkansson and Jensen 2008).

If they are adapting to zoo conditions, might we consider these animals to have good welfare, because they are coping with the new captive environmental factors? From an 'animal natures' perspective, any changes to animals that occur as a consequence of captivity should be investigated in terms of their potential to compromise welfare, because they compromise the nature of the animal. This matter is very complex, because adaptations to captivity are usually deemed to improve the welfare of captive animals: animals that do not adapt do not survive, or do so badly (and probably with impoverished welfare); however, animals that have adapted, (i.e. domesticated animals) usually have successful reproductive lives and show a reduced stress response to captive environmental stressors (Broom and Johnson 1993). But while their welfare may be improved while the animals are in captivity, if the function of the captive population is to provide a pool of animals for **reintroduction** at a later date, then it is likely that the captive environmental pressures to which they have now become accustomed will not be like those that they will experience in the wild (Frankham 2008). So, in the short term (while they live in captivity), their welfare may be improved through adaptation, but, in the long-term (if animals are reintroduced back into the wild), their welfare—and indeed their survival—may be compromised.

From a conservation point of view, this process of passive domestication may present problems. Certainly, captive management programmes attempt to reduce any adaptation to captivity in terms of the genetic integrity of animals

(see **section 9.2.4**), but they do not necessarily prevent changes in behaviour (see also **section 10.5**), although appropriate husbandry and enrichment might go some way to mitigating it (Shepherdson 1994) (see **section 7.5**).

Consider, for example, the process of **socialization**, whereby animals routinely interact with people and become familiar with them (Mellen and Ellis 1996) (**Fig. 7.10**), leading to changes in the human–animal relationship (**Chapter 13**). Here, we can see that there is a potential conflict between conservation goals and welfare goals. Socialization is usually considered to impair reintroduction success, so attempts have generally been made to limit its impact on captive animals, but especially on animals destined for reintroduction.

The few studies that have investigated the influence of socialization, however, have shown that it can improve the welfare of animals while they are in captivity. In small exotic felids, for example, socialization resulting from increased levels of interaction with keepers was associated with elevated rates of reproduction and a reduction in the cats' stress responses (Mellen 1991). Similarly, there was a significant positive correlation between breeding success in the cheetah and the predictability of the keepers' routine and the regularity of the cleaning and feeding regime (Baker and Pullen, submitted). However, there can also

Figure 7.10 All animals in zoos will be exposed to people to varying degrees, whether managed in a 'hands-off' or 'hands-on' style. Typically, contact between keepers and animals occurs during (a) routine procedures, when they are moved between enclosures, fed, or cleaned. More extensive interactions might also occur as a consequence of (b) training, and (c) providing enrichment. Contact with keepers will lead to the process of socialization, as during (d) this penguin parade. (Photographs: (a) and (b) Mel Gage, Bristol Zoo Gardens; (c) Emma Cattell, Howletts and Port Lympne Wild Animal Park; (d) Jeroen Stevens, Toba Aquarium, Japan)

be negative repercussions associated with changing the human–animal relationship. For example, too much close contact with humans can impede reproduction and put keepers at risk of injury (this is covered in more detail in **Chapter 6**).

This adaptation to captivity has other consequences on the biological functioning of the animals, including more generalized deleterious impacts on their morphology, physiology, and genetics, thus also presumably impacting negatively on their welfare. **Inbreeding depression** becomes more likely in successive generations of captive populations, because there is a closed **gene pool**, usually made up of few **founders**.

Inbreeding is almost always detrimental to welfare. For example, inbreeding depression was negatively correlated with **longevity** in wolves *Canis lupus* and lynx *Lynx lynx* in Nordic zoos (Laikre 1999). Similarly, Wielebnowski (1996) found that offspring from closely related cheetah were more likely to be stillborn or suffer congenital defects compared with the offspring born to unrelated cheetah. (The management of species to decrease inbreeding is explored more fully in **section 9.2.2**.)

There are also morphological changes that have been observed in a variety of species and which have occurred over successive generations in captivity. Some of these have been reviewed by O'Regan and Kitchener (2005), who have attributed the changes to a variety of different factors, including dietary deficiencies, behaviour, and age. Many animals live longer in captivity than they would in the wild, and some of the morphological changes that they experience could impair their survival in the wild if they were to be released. **Carnivores**, for example, might have difficulty killing or processing prey. The jaws of American alligators *Alligator mississippiensis* have become shortened in captivity, although their heads are broader and their bodies more robust than those of wild alligators (Erickson *et al.* 2003). On the other hand, the skulls of leopards *Panthera pardus*, lions *Panthera leo*, and tigers *Panthera tigris*, appear to have become larger (O'Regan 2001; Duckler 1998) (**Fig. 7.11** and **Table 7.2**). The cause and impact of these morphometric changes in zoo-housed carnivores is unclear. It is unlikely that **nutrition** is the cause of this deviation from the wild-type
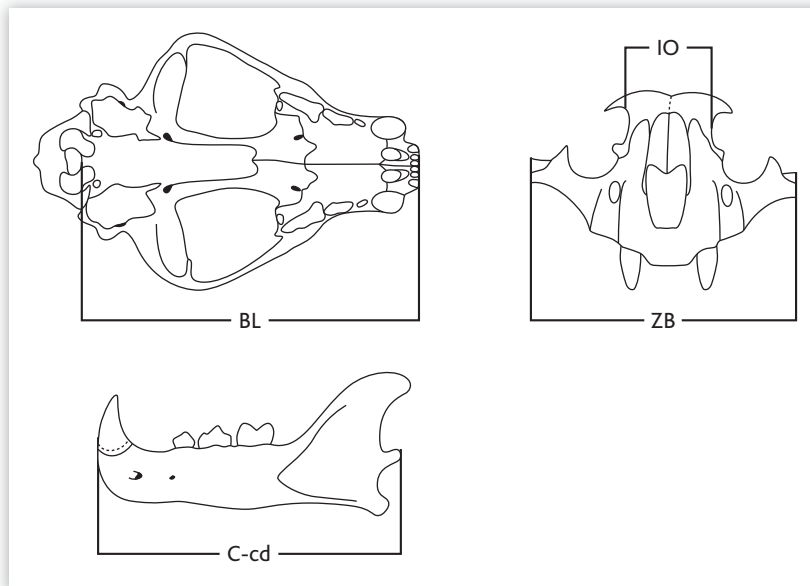
Figure 7.11 A study of the skulls of zoo-housed lions *Panthera leo* and leopards *Panthera pardus* revealed that one cranial dimension, zygomatic breadth (ZB), was significantly larger in captive animals compared with measurements taken from the skulls of wild conspecifics (see **Table 7.2**). (The measurements of three other dimensions were not significantly different.) (From O'Regan 2001)

Species	Sex	Wild (*N*)	Zoo (*N*)	Wild median	Zoo median	Alpha
P. pardus	Male	19	5	135.0	137.0	0.6695
	Female	13	4	119.0	137.5	0.0312*
P. leo	Male	11	8	223.0	249.5	0.0289*
	Female	11	9	198.0	210	0.0365*
P. leo	Male	6	5	233.5	261.5	0.0137*

Table 7.2 Significant differences in the zygomatic breadth (ZB) of skull measurements in zoo-housed and wild carnivores
From O'Regan 2001
*<0.05
Note: Mann–Whitney U test results for the difference between modern captive and wild lions and leopards.

skull because, in this case, we would expect an increase in the overall size of the skull. Anecdotally, it has been suggested that these changes may have arisen out of 'lack of use', because many captive Carnivores do not need to bring down large-bodied prey or mechanically process them as they would in a live-kill situation (although some enrichment does aim to simulate these behaviours).

One pragmatic solution to the potential advantages and disadvantages associated with adaptation to captivity would be to designate individual animals, as far as possible, as being destined either for reintroduction or for a life in captivity, considering the roles animal fulfil in captivity (Watters and Powell 2012). As this is unlikely to be implemented, however, some sort of compromise involving degrees of domestication might be the best recommendation, whereby some natural behaviour is promoted but the animals still interact with keepers (Newberry 1995). On this basis, the benefits of adaptations required for life in the wild, as well as those that may better serve life in captivity, can both be enjoyed.

7.4 Indices used to evaluate zoo animal welfare

Many people feel justified in judging the welfare of zoos animals according to what they see when they pass an enclosure. But this glimpse does not usually tell the visitor very much, and it certainly does not enable them to interpret whether the animal is suffering from environmental challenge or behavioural restriction, or is adapting to its captive surroundings.

There are many indices that can be used to assess zoo animal welfare, including the diversity of the animal's behavioural repertoire, its enclosure use, the extent of its social interactions, its **life history traits**, and many more. Most zoo visitors are unaware of these indices and, instead, judge welfare by the level of activity that they observe in the animal and whether its enclosure is aesthetically pleasing (Melfi *et al.* 2004a; **Fig. 6.9**). Given the complexity of the relationship between activity levels, enclosure style, and animal welfare, however, using only these to assess welfare seems highly unreliable.

Establishing which indices can be used to evaluate zoo animal welfare is not easy. Some of the indices may only indicate that an animal has responded to a stimulus, but this does not necessarily reflect changes in the animal's welfare. Similarly, deviations from normal functioning, whether behavioural or physiological, do not necessarily indicate suffering (see **section 7.2**). Therefore it is essential that any indices that are used to evaluate animal welfare are first validated. Validation is most commonly accomplished via two main routes. Animals can be subjected to an 'almost certain' stressful event or aversive stimulus, and a record taken of which indices change
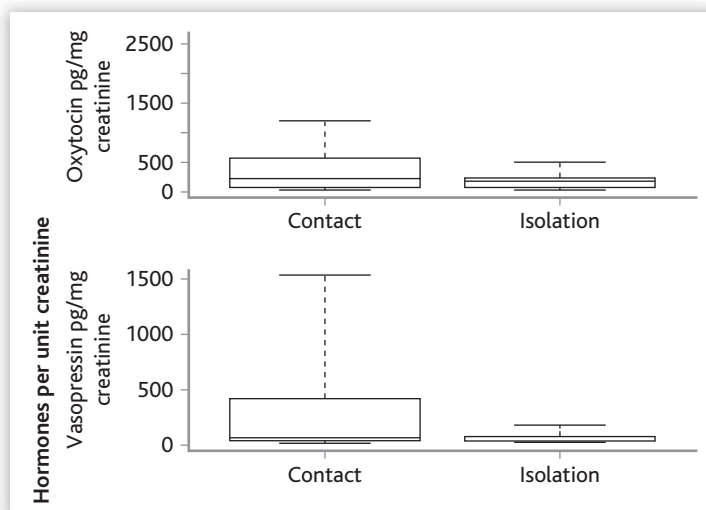
Figure 7.12 Seltzer and Ziegler (2007) found significant differences in hormones measured in voided urine samples; marmosets in isolation had significantly lower levels than those marmosets which had social contact. (From Seltzer and Ziegler 2007)

and how. An example of this is taking measurements when animals are being transported, an event that is regarded by many as stressful (see **section 6.3.2**). Theoretically, indices can also be measured when animals are thought to be in good circumstances, and these then would indicate positive welfare. More recently, however, parameters associated with good welfare are being studied by collecting data during times of positive physiological and social situations that are indicative of good welfare. For example, Seltzer and Ziegler (2007) measured levels of two hormones associated with good welfare—oxytocin and arginine vasopressin[8]—to assess the impact of social isolation on welfare in a troop of common marmosets *Callithrix jacchus* (**Fig. 7.12**). Measurement of these indices has been expanded to measure welfare and positive emotion in other species (e.g. dog (Mitsui *et al.* 2011)). Alternatively, new indices can be validated by monitoring them alongside other indices that have previously been validated as accurately monitoring animal welfare. For example, Plowman *et al.* (2005) were interested in studying whether management changes to a troop of Hamadryas baboons *Papio hamadryas* affected their

welfare (**Fig. 6.21**), and to find out they measured **self-directed behaviours** (**Fig. 7.13**). The expression and frequency of these behaviours had already been validated as a reliable index of welfare, because previous studies (e.g. Maestripieri *et al.* 1992) had shown that they correlated well with other behavioural and pharmacological indices of poor welfare.

It is necessary to collect data for many different indices because zoo animals represent a diverse array of species and they are likely to be affected differently by environmental factors. Interpreting this complexity can be difficult. For example, oral and locomotor stereotypies in giraffe *Giraffa camelopardalis* and okapi *Okapia johnstoni* were found to be affected by different combinations of environmental factors (Bashaw *et al.* 2001). We strongly recommend that several indices are used whenever trying to assess animal welfare, particularly in the zoo setting.

A final consideration is the time frame over which the welfare of the animal is being assessed. In **section 7.3.3**, we said that welfare could be considered in both the short and long term, with regard to the impact of adaptations made by the animal to captive environmental variables. The

---

[8] **Oxytocin** and **arginine vasopressin** are both peptide hormones secreted by the posterior pituitary. Although both have a number of physiological effects in the body, both are also thought to be involved in social interactions and the mediation in the brain of positive social behaviours.
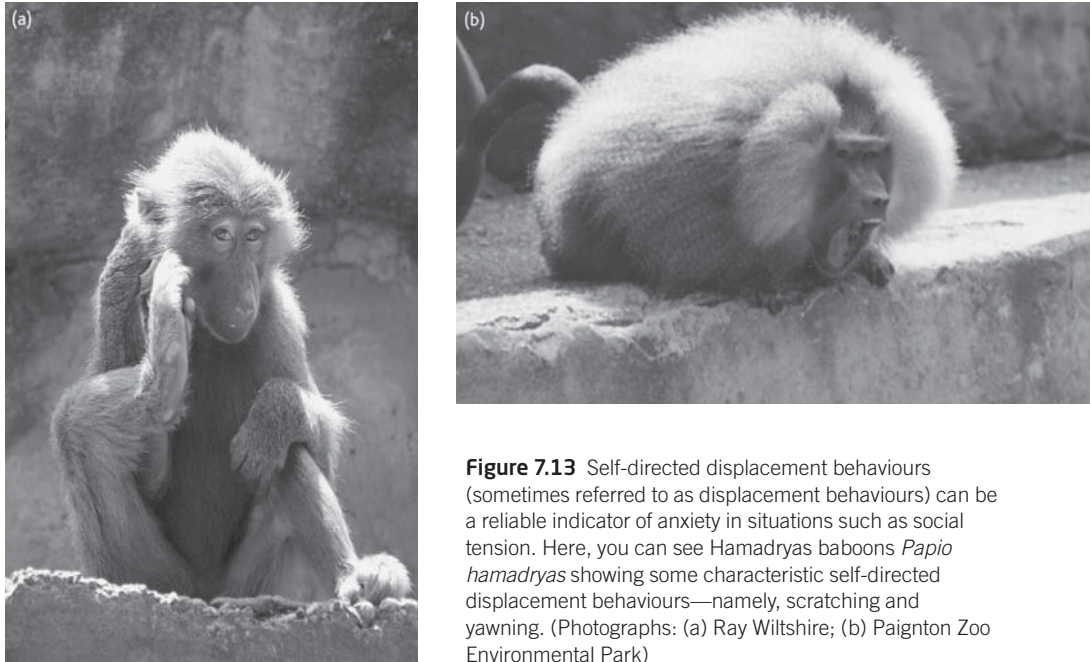
Figure 7.13 Self-directed displacement behaviours (sometimes referred to as displacement behaviours) can be a reliable indicator of anxiety in situations such as social tension. Here, you can see Hamadryas baboons *Papio hamadryas* showing some characteristic self-directed displacement behaviours—namely, scratching and yawning. (Photographs: (a) Ray Wiltshire; (b) Paignton Zoo Environmental Park)

duration of the stimuli that affect animal welfare can also be long or short term, and thus give rise to chronic or acute responses, as mentioned in **section 7.2.2**.

Table 7.3 illustrates some of the physiological and behavioural changes that are associated with acute and chronic stress responses.

7.4.1 Life history variables and events

If we follow the 'animal bodies' approach, we might consider animal welfare to be impoverished if an animal is not able to cope in its environment, which, for our purposes, means that it has not been able to adapt to the captive environment. An animal that has successfully adapted to stimuli within the captive environment might be expected to function as well in captivity as it does in its native habitat, thus giving rise to wild–captive comparisons of those parameters that represent success. But we might also consider that the animal has evolved to function and cope with some significant stressors; thus if comparable stressors are experienced in captivity, these might not necessarily compromise welfare (Barnard and Hurst 1996).

Generally, a successful animal is considered to be one that is able to get its genetic material into the next generation. Measures of **fecundity**[9] and longevity are likely to be indirectly proportional to genetic success, both in the wild and in captivity. It also makes intuitive sense that these measures will also indicate the extent to which the animal is able to cope in captivity, and thus indicate its welfare state. Fecundity is a measure of reproductive success that can be calculated in various ways, representing greater degrees of rigour: it can be calculated as the number of offspring an animal has produced, or as the number of offspring produced

---

[9] According to demographers, fecundity is a measure of reproductive *potential*, so can be measured by the number of gametes produced by an organism. But biologists often use fecundity to mean actual reproductive success, i.e. surviving offspring produced, much the same as fertility. As biologists, quoting lots of biological papers, we'll stick to the latter definition.

	Short-term symptoms	Long-term symptoms
Behaviour	Fight or flight Cessation of 'normal' behaviours	Aggression Stereotypies Apathy Self-harming Protective behaviour
Gross biological indices	↑ Heart rate, respiration, and body temperature	↓ Reproductive success, life expectancy, and growth
Endocrine function	Adrenaline Noradrenaline Adrenocorticoids Prolactin	Endogenous opioids Glucocorticoids
Nervous/immune system	Adrenaline Dopamine	Immunosuppression ↑ Incidence of disease
Enzymes/metabolic products in the blood	Renin (from the kidney)	Creatine kinase (from the heart)

Table 7.3 A summary of the symptoms expected according to whether stress is short or long term*

*After Broom and Johnson (1993)

Note: The impact of stressors varies according to how long they persist. Short-term stressors are associated with acute stress, whereas prolonged stimulation/stress leads to chronic conditions.

that survive (usually measured up to 30 days, up to 1 year, and then to age of sexual maturity), or the number of offspring produced that were themselves able to reproduce successfully. Longevity is the length of time that an animal lives.

Although animal welfare should be considered from the perspective of the individual, viewing life history traits for a group of animals can provide information about the extent to which the group (due to specific environmental conditions in one location) or whole **taxa** (due to shared species differences and thus ability to cope) are able to succeed, termed the comparative approach by Mason (2010). These types of analyses can highlight animals that have specialist lifestyles and which require certain characteristics from their environment, so if they do not gain these characteristics, they are unable to adapt and therefore will not succeed. Equally, these types of analyses can identify ways in which captive environments can, and should, be modified to facilitate success. Clubb and Mason (2007) have used this approach to study the

ability of Carnivores to succeed in captive conditions, using measures of longevity and the development of stereotypies to assess their welfare in captivity. They considered that animals with relatively short lives who performed stereotypies had poor welfare because they were unable to adapt to captivity.

As with all indices used to assess animal welfare, there are some limitations to using life history variables in isolation. The fecundity and longevity of an individual can be affected by many variables, and these may or may not necessarily be related to welfare. It is common for animal management programmes to adopt strategies in which animals are not provided with the opportunity to breed, for example because of limited space (see **section 9.7**). Restricted breeding may have a deleterious impact on welfare, but would need to be considered differently from simplistic fecundity comparisons. Equally, an animal may die as a result of disease, or socially inflicted wounds, or planned euthanasia as part of a captive management programme; thus

mortality or fecundity *per se* may not be robust measures of welfare taken on their own, or indeed over a certain threshold. Obviously, if the population doesn't breed or all die young, there are likely to be problems which are almost certain to compromise welfare. Over a certain threshold, however, these indices are likely to lose some of their value, i.e. they are not exponentially related to welfare, whereby maximum fecundity and longevity equal optimal welfare (see **Box 7.4**). Therefore it is necessary, when using these indices as a measure of animal welfare, to consider details of the animal's life and its captive management as well, even though this can make the accurate analysis of these types of variables time-consuming (e.g. Clubb *et al.* 2008 and 2009).

7.4.2 Biological processes

The most widely adopted approach to assessing animal welfare is to monitor an animal's biological function, which can provide an indication of why an animal succeeds, or otherwise, in thriving in its environment. There are many biological processes that underpin biological function, but most studies of animal welfare choose to examine endocrine function because hormones, particularly cortisol, mediate the animal's reaction to stressful situations (**Box 7.3**). But other biological processes, such as the activity of the immune and nervous systems, also provide information about the animal's ability to cope within its environment. These physiological indices are usually studied in conjunction with observations of behaviour.

Biological processes are essential for survival, and an animal's responses to stimuli (sometimes termed 'stressors' or 'environmental challenge') do not necessarily represent welfare infringements. They may only reflect routine homeostatic function; glucocorticoids, for example, are important in energy metabolism as well as in mediating the stress response. Because of this, the interpretation of these indices in relation to animal welfare requires some caution, because changes in different parameters do not necessarily reflect animal suffering *per se*. There are also many other factors, other than the animal's welfare, that affect changes in biological processes, including time of day, reproductive status, individual differences, etc.

Therefore the value of using biological processes to measure animal welfare is strengthened by considering multiple indices in combination. This is exemplified by the way in which endocrine function is measured and how changes in cortisol concentration are interpreted in conjunction with other welfare indices. For example, behavioural observations and the non-invasive monitoring of cortisol have been used to evaluate the welfare of a number of zoo-housed species, including giant pandas *Ailuropoda melanoleuca* (Liu *et al.* 2006; Powell *et al.* 2006), clouded leopards *Neofelis nebulosa* (Wielebnowski *et al.* 2002), black rhinoceros *Diceros bicornis* and white rhinoceros *Ceratotherium simum* (Carlstead and Brown 2005), and Indian blackbuck *Antelope cervicapra* (Rajagopal *et al.* 2011).

7.4.3 Behaviour

Observations of animal behaviour are non-invasive and therefore intuitively a method favoured by many animal welfare scientists. Behavioural expression provides a measure of animal welfare that overlaps all four approaches to the study of animal welfare:

- social interactions, problem solving, and the study of animal learning can provide some indication of the animal's mind;
- the development of abnormal behaviours may indicate that the animal's biological processes are unable to function within its current environment;
- an animal's inability to express behaviours seen in its wild counterparts indicates changes in nature;
- in some instances, it can be justified to interpret the function of behaviour by drawing on the knowledge gained from other species and using analogy.

Box 7.3 THE USE OF CORTISOL AS A MEASURE OF ANIMAL WELFARE

The measurement of cortisol, and its metabolites, has long been recognized as a reliable indicator of adrenal function and thus provides information on an animal's stress response (see **Box 7.2**). The non-invasive assessment of cortisol has been conducted using faecal samples in a wide variety of non-domesticated species, including Alaskan sea otter *Enhydra lutris*, Roosevelt elk *Cervus canadensis roosevelti*, gerenuk *Litocranius walleri*, and Northern spotted owl *Strix occidentalis caurina* (reviewed by Wasser *et al.* 2000). Other non-invasive techniques include the use of urine (for example, in elephants—see Brown and Wemmer 1995) and saliva (for example, in Asian elephants *Elephas maximus* and Indian rhinoceros *Rhinoceros unicornis*—Menargues *et al.* 2008). Davis *et al.* (2005) provide an example of a zoo study, using cortisol as a welfare indicator, of the effect of visitor numbers on spider monkeys *Ateles geoffroyi rufiventris.* They found that increased visitor numbers paralleled an increase in cortisol levels compared with instances in which there were no visitors present in the zoo.

Cortisol is released in increased quantities because of activity of the HPA axis during periods of stress; it is also involved in other physiological mechanisms. Elevations in cortisol associated with a stress response may also occur after a meal has been eaten or when an animal is active, and may be affected by the animal's rank, sex, or age (Lane 2006). Furthermore, variations in cortisol levels can occur due to diurnal and seasonal rhythms, temperature, humidity, and several other factors relating to the animal and its environment (Mormede *et al.* 2007). Care should also be taken to ensure that non-invasive samples are handled and processed appropriately to ensure accurate estimations of cortisol concentrations. For example, Millspaugh and Washburn (2003) showed that glucocorticoids were not necessarily evenly distributed in faeces, so all voided faeces should be mixed thoroughly and a representative sample taken to reduce the likelihood of bias in the sample. Furthermore, cortisol levels assessed from faecal and urine samples represent the averaged

stress level for the animal, as the faeces and urine will take time to travel through the gastrointestinal tract and thus will absorb cortisol over time, whereas cortisol levels calculated from saliva samples provide information on the current stress status of the animal, as cortisol released directly into the blood stream is detectable in saliva. Therefore chronic stress levels can be more readily evaluated from faecal and urine samples, whereas acute stress levels are best calcuated from saliva.

Despite the many factors that can affect the production and assessment of cortisol concentration, it is still recognized as being an accurate and helpful measure of stress, and thus of animal welfare. When using cortisol as a welfare indicator, consideration of its limitations should be borne in mind and complementary animal welfare indicators measured as well (Millspaugh and Washburn 2004; Lane 2006). Recent studies have also identified that cortisol levels are significantly correlated with personality dimensions, such that in a study of African elephants, those animals which were considered fearful were found to have higher cortisol levels, whereas social and aggressive animals had lower cortisol levels (Grand *et al.* 2012). Methods used to measure an animal's biological function typically follow standardized protocols that enable the collection of reliable, objective, and repeatable empirical data. These measures are comparable within and between animals, and can be easily scrutinized, which makes them ideal for the scientific study of animal welfare, and this is probably why their use has proliferated in this field. Historically, measuring physiological indices usually required some degree of invasive procedure through blood sampling, biopsies, or by obtaining information at **post-mortem** after the death of the animal. This has the obvious disadvantage that the data collection method used to monitor animal welfare may itself compromise welfare or, at the very least, confound the results. Thankfully, technological advances have now gone a long way towards ameliorating this problem, because many biological processes can now be monitored via non-invasive approaches.

For a long time, the study of stereotypies in zoo-housed animals has been seen as the chief indication of impoverished welfare. But the interpretation of the performance of stereotypical and other abnormal behaviours is not always clear-cut, although the performance of them does reduce **behavioural diversity** and thus can lead to behavioural restriction (Golani *et al.* 1999). (The topic of stereotypies is explored further in **section 4.4.3**.) It should also be noted that whether behaviours are referred to as 'normal' or 'abnormal' is also not straightforward; this is discussed in **section 8.3.2**.

As with the use of other measures of animal welfare, behavioural indices should be validated to ensure that their interpretation is justified. Castellote and Fossa (2006) justified their use of underwater vocalizations as a welfare indicator in beluga whales *Delphinapterus leucas* because they were found to decrease both after the introduction of four harbour seals *Phoca vitulina* into the exhibit and after air transportation to new facilities; transportation has been found to compromise welfare in a variety of species (reviewed by Broom 2005). Vocalizations have been shown to give a useful indication of animal welfare in other species as well, indicating both good and poor welfare (Boissy *et al.* 2007; Burman *et al.* 2007).

7.4.4 Health

Poor health can impoverish animal welfare through a variety of routes, not least because it limits an animal's ability to cope with challenges in its environment, can restrict behavioural expression, and can result in pain. There are several main ways in which to evaluate health status in zoo animals and thus infer something about their welfare, and much of this is discussed in **Chapter 11** on 'Health' (**Fig. 7.14**).

The daily monitoring of animals, which is usually initiated to monitor animal health, can provide a helpful insight into what is considered normal for that animal or species, and deviations from these 'norms' alert zoo professionals to the potential that health and/or welfare may be compromised (see **section 5.6.6**). The sorts of information
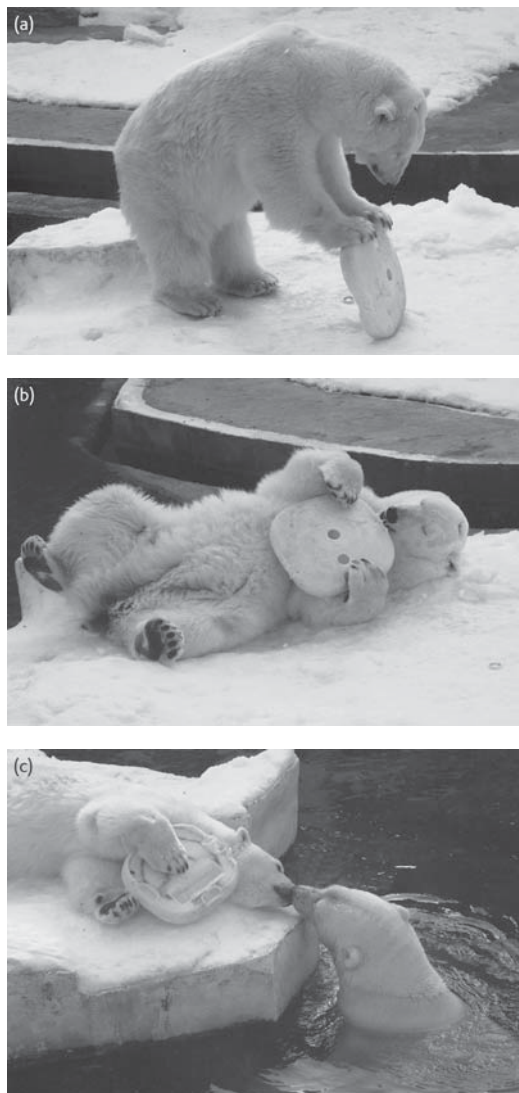
Figure 7.14 Given that there is evidence from post-mortem results that old Carnivores in zoos can suffer from skeletal problems, it may be prudent to ensure that these animals are provided with plenty of physical exercise so that they remain physically fitter for longer (although this will not stave off ageing indefinitely). (Photograph: Warsaw Zoo)

that can be monitored include weight, condition, interactions with conspecifics, feeding behaviour, and fluctuations in these variables (e.g. Whitham and Wielebnowski 2009). Retrospective information about animal welfare can also be gained from analyses of post-mortem results, which provide invaluable details about the condition and welfare

of an animal during its life (see **section 11.4.8**) and how they affect its physical functioning. Such studies, which are not possible while the animal is still alive, can provide information that may have gone unnoticed because few visible characteristics existed. For example, during post-mortem examination of many zoo-housed Carnivores, Kitchener and MacDonald (2004) discovered that most old animals had severe spine deformities which, they suggested, would have been painful during the life of the animals. These data initiated the discussion that old animals in zoos may have poor welfare and that longevity is not necessarily a goal that should be sought, but rather quality of life (see **Box 7.4**).

7.4.5 Asking the animals themselves?

To understand how an animal is feeling and what implications this has for animal welfare, the following types of questions can be asked.

- Is the animal aware?
- Does it know that it is suffering or understand that another animal is suffering?
- Does it remember past events or fear future events?

Answering these kinds of questions and measuring the subjective experiences of animals is difficult, as we explored earlier; however, **preference tests** have been proposed as a method that can indirectly tell us how an animal feels (Duncan 2005; reviewed by Fraser 2008).

Preference tests involve the simultaneous presentation of different resources to an animal, and the resource chosen is assumed to be that which it prefers and therefore wants. This method provides us with a mechanism by which to interpret how an animal perceives its own needs, in terms of what it wants from its environment. In order to evaluate animals' preferences fully, it is very important that we do not underestimate their environmental complexity and/or needs, so we should provide them with sufficient options from which to choose and indicate to us their preferred

resource (Fraser and Matthews 1997). The number and appropriateness of the resources presented determines the value of the results. Simply learning which of two resources an animal prefers may be of little value if neither of the resources represents what the animal actually 'likes'. The preferred choice may also be affected by previous experience, genetic predisposition, reproductive status, season, time of day, and many other factors; furthermore an animal's use of a new resource may reflect its tendency either to avoid or to use novel resources. Thus we should be cautious in our interpretation of the choices made by animals in these types of studies, because an animal's priorities may change.

A variation of the preference test is the **strength of motivation test**, which assumes that an animal's willingness to 'work' for a resource reflects its level of motivation to gain the resource or carry out the behaviour. Elegant experimental designs have been used to calculate how much effort (time or energy) an animal is willing to expend to get access to a resource. This provides a measure of the strength of the animal's preference for a resource, and underpins **behavioural economic theory**. Dawkins (1983), a pioneer in this area, considered there to be a parallel between the choices made by human shoppers (in economic theory) and the choices made by animals when choosing between resources. This method provides a way in which to interpret the animals' preference for different resources, when they are provided both at different times during the day and throughout its life. There are several further variations of the preference test, developed to measure the strength of an animal's preference, as follows.

1. Will an animal learn a behaviour in order to gain the resource? If not, the demonstrated preference for that resource is considered weak.
2. An **obstruction test** puts something such as a door between the animal and its resources, and determines how hard the animal is willing to work to get around the obstacle to gain the resource.

3. Animals are offered a choice of resources, but are restricted by the amount of time that they have with them; the assumption here is that, as the time allowed to gain the resources diminishes, the animal will choose the resources that it most prefers or needs.

4. **Aversion tests** study if the animal is willing to choose to undergo something unfavourable, such as an electric shock, to get to a resource.

Some preference testing in zoo animals has been undertaken to determine which foods or enclosure locations are most highly sought after (e.g. Ogden *et al.* 1993; Ludes and Anderson 1996). Animals in zoos have also been observed to show a preference to gain food, using behaviours that they would express in the wild. Elson and Marples (2001) found, in several parrot species, that the birds prefer food if it is presented in a manner that reflects their 'natural' feeding habits. Instead of feeding from dishes in their enclosure, or from enrichment devices representing alternative feeding styles, the parrots would use the enrichment devices that required the expression of their natural species-specific feeding behaviours. Thus, golden-shouldered parrots *Psephotus chrysopterygius* selectively used hanging branches with seeds glued to them, which enabled them to employ the sorts of manipulative behaviours that are used by their wild counterparts to gain food from seed pods and/or grass heads. Scarlet-chested parrots *Neophema splendida*, on the other hand, feed mainly on the ground and they showed a preference for foraging trays placed on the ground. This is also an example of **contrafreeloading**—a phenomenon that is explored in more detail in **section 8.6.3**. More recently, attempts have been made to construct situations in which the motivation of zoo animals can be tested. For example, Nicholls (2003) measured the motivation strength

Figure 7.15 There are many studies of preference tests for mammal and bird species, but few for other taxa. At Paignton Zoo Environmental Park, the preferences of tortoises were measured by providing them with different resources, accessible by climbing up a ramp. The tortoises were willing to walk up a steeper ramp to gain access to their favoured resources. (Photograph: Paignton Zoo Environmental Park)

of Hermann's tortoises *Testudo hermmani* by providing them with a slope, on top of which were different resources. By changing the gradient of the slope, she was able to find out how steep a slope the tortoises would climb in order to get to the resource. She found that the tortoises would climb more quickly and up steeper slopes for sand than for twigs (**Fig. 7.15**). This is still a relatively underexplored area, which offers many research opportunities.

7.4.6 Cognition

If we follow the 'animal minds' approach to animal welfare, we find that current trends in this field are in favour of some attribution of emotion to animals (see **section 7.2.1**) and to some extent sentience (Webster 2006). The extent of their cognitive capacity, which can be measured by the existence of **theory of mind**[10] or self-awareness, is studied in this field to provide a better understanding of the degree to which the animal is able

---

[10] **Theory of mind** refers to an individual's knowledge of another individual's mental processes. Self-awareness is having knowledge of oneself as an individual, distinct from other individuals. Both of these are regarded as higher-order cognitive abilities and the extent to which animals possess them is controversial.

to experience emotion and therefore what influence this might have on welfare.

Gregory (2004) suggested that the complexity of an animal's mind is probably paralleled by its capacity to learn. Thus, learning capacities that go beyond simple stimulus–response connections may be indicative of higher mental processes and potentially suggest a greater capacity for emotion. As we, ourselves, are animals with complex minds and a high capacity to learn, we tend to put primates at the pinnacle of evolutionary intelligence whenever we think of differences in animals' abilities. Interestingly, however, as more data are amassed, the cognitive capacities of many non-primate species are being revealed to rival—or even surpass—that observed in non-human primates. For example, sea lions *Zalophus californianus* have been observed to learn **reverse-reward contingency tasks** at a more rapid rate than primates (Genty and Roeder 2006). In one task, the sea lions were required to learn that if they chose a smaller portion of fish when offered a choice, they would, in fact, receive a larger portion of fish to eat as a reward; this is a demonstration of self-control that implies an understanding in the animals about gaining a delayed reward (**Fig. 7.16**).
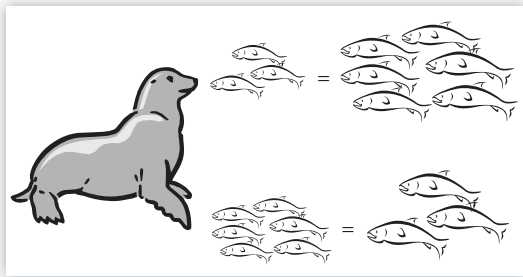
Figure 7.16 As the cognitive abilities of more species are tested, the results are challenging the long-held belief that primates are at the 'top of the intelligence pyramid'. For example, sea lions can learn to choose a smaller portion of fish, in order then to receive a reward of a larger portion of fish. This complex task, choosing a smaller portion even though a larger portion is also available, was not achieved by non-human primates during the same trial.

The complexity of animals' social systems and their interactions with the environment have also been used as an indicator of cognitive ability, because it is suggested that both these factors would need to increase in parallel. For example, Simmonds (2006) reviewed the literature available on cetaceans and suggested that behavioural measures observed in these animals corroborated the belief that they had high levels of intelligence, and thus had the capacity to suffer. Similarly, Douglas-Hamilton *et al.* (2006) used extensive behavioural observations to assert that elephants can show a variety of emotions, and have a general awareness and curiosity about death of their conspecifics. This methodology follows closely that adopted by Griffin (1992), a proponent of the 'animal minds' approach to animal welfare, who used a great deal of anecdotal information about animal behaviour as evidence for the existence of animal minds.

A fairly recent approach being employed to study animal emotion uses operant conditioning techniques to determine whether animals are 'optimists' or 'pessimists' (Harding *et al.* 2004). For example, Burman *et al.* (2008) trained laboratory rats in a spatial discrimination task, where they were rewarded in one location and not in a second. Later, they were presented with ambiguous stimuli in one of three locations: one was located half-way between the 'extreme' rewarded and unrewarded sites, and the remaining two stimuli were positioned between the mid-way point and the two extreme sites. Pessimistic animals would be expected to more readily approach the stimuli nearest the unrewarded site, whereas optimistic animals would more readily approach the stimuli nearest the rewarded site. This method of animal emotion assessment, testing for cognitive bias, has been adopted to evaluate many different species (Mendl *et al.* 2009). However, studies are demonstrating that changes to housing and husbandry do have significant impacts on animal emotion; for example, environmental enrichment was found to induce optimism in laboratory-housed rats (Brydges *et al.* 2011) (**Fig. 7.17**).
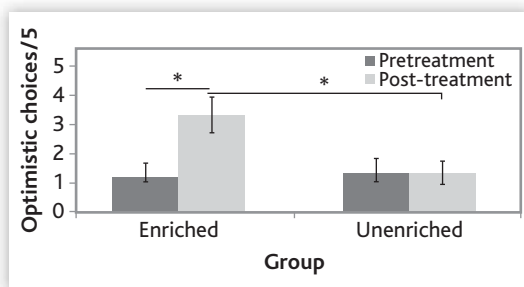
Figure 7.17 Rats provided with enrichment were shown to make significantly more optimistic choices, as measured by means of cognitive bias studies. (From Brydges *et al.* 2011)

7.5 Meeting the needs of zoo animals

Our knowledge of zoo animal welfare has advanced greatly in recent years, as the study of their needs, and how they can be compromised in captivity, has been addressed more and more in research. Furthermore, the appropriate monitoring of validated welfare indices permits the identification of factors within the zoo environment that may be compromising welfare and therefore allows remedial action to be taken in an attempt to reduce the impact of these factors.

Within the field of animal welfare science more generally, advances in knowledge have not necessarily been mirrored by the implementation of appropriate practices to ensure good animal welfare (Millman *et al.* 2004). Dawkins (1997) suggested that this lag between knowledge and implementation was due to the differing perspectives of the many different parties involved, who included the animal welfare scientists, the public, and politicians. This was because scientists needed more time to appreciate fully the complex issues underlying the factors that affect animal welfare, while the public were not harnessing their power enough to influence change through consumer pressure and the politicians were not always supportive of legislative change (Dawkins 1997). On the basis of this, we might suggest that zoo animal welfare could be greatly improved if

more dedicated welfare scientists were to study animals in zoos, if there were continued pressure from 'informed' zoo visitors for better standards, and if there were greater harmonization of legislation and regulation promoting zoo animal welfare worldwide.

More pragmatically, and within the scope of those currently working in zoos, a series of steps can be outlined that, if adopted, could greatly enhance animal welfare. These involve identifying what the animal's needs are, minimizing the risks to animal welfare, using a logical and consistent framework to decide how to resolve conflicts between welfare and the other goals that the zoo aims to achieve, improving our knowledge of animal welfare science and how to best achieve it, and, finally, using this information to inform legislative reform and to support enforcement.

7.5.1 Five freedoms

The **five freedoms** encompass the basic needs of animals and, if they are satisfied, they should ensure an adequate level of welfare (see **Table 7.4** and **Fig. 7.18**). They were originally conceived as a tool to ensure a minimum standard for farm animal welfare: a British government Farm Animal Welfare Advisory Committee chaired by Professor Brambell, in 1965, proposed that all farm animals should be able to '*stand up, lie down, turn around, groom themselves and stretch their limbs*' (FAWC 2012). Subsequently a reincarnation of the five freedoms (**Table 7.4**) has become ubiquitous in the assessment of welfare for animals worldwide, whether kept in zoos, in laboratories, or as pets, and is the cornerstone of many welfare strategies at a national and international level (e.g. the Food and Agriculture Organization of the United Nations (Vapnek and Chapman 2010)). Indeed, the 'five principles' of zoo animal care set out in the Secretary of State's Standards of Modern Zoo Practice (Defra 2012a), which we saw in **section 3.4.2**, are derived from the five freedoms.

Although the five freedoms provide a good starting point from which to consider animal

Freedom	Provision	Cross-reference
From thirst, hunger, and malnutrition	Ready access to fresh water and a diet designed to maintain full health and vigour	**Chapter 12**
From discomfort	Provision of an appropriate environment including shelter and a comfortable resting area	**Chapter 6**
From pain, injury, and disease	Prevention or through rapid diagnosis and treatment	**Chapters 6** and **11**, and **Box 7.1**
To express natural behaviours	Sufficient space, proper facilities and company of the animal's own kind	**Chapters 4, 8,** and **11**
From fear and distress	Assurance of conditions that avoid mental suffering	**Section 7.3.1**

Table 7.4 FAWC five freedoms (2012)

Note: The five freedoms provide a guide to conditions which, with compliance, would result in minimum standards for captive animal welfare. In zoos, the five freedoms can be accomplished through best practice, which has been reviewed in other chapters within this book.

welfare, there are concerns that the use of minimum standards can sometimes prohibit advances in knowledge or the promotion of higher standards (Melfi 2009). This is because minimum standards can sometimes be viewed as a benchmark to be aimed towards, rather than a standard beyond which to go. In addition, they aim to prevent observed changes in those indices that are associated with poor welfare (for example, the presence of stereotypies or weight loss), rather than aiming to promote signs of good welfare (such as the expression of behavioural diversity or psychological well-being). Furthermore, Mench (1998) suggested that the continual study and assessment of animal suffering, rather than animal well-being, would not ultimately lead to major improvements in welfare. Essentially, animal welfare should not be merely the removal of suffering, but the provision of pleasure (Duncan 2006). Good zoo animal welfare can be achieved through proactive responsibility for enhancing the daily lives of animals in our care, and this can be initiated by taking steps to ensure that risks to welfare are not present in the first place. Thus,

the aim is to strive to make animals happy and not simply to ensure that they do not suffer.

7.5.2 Minimizing risks to welfare

In **section 7.3**, we considered factors that might compromise the welfare of zoo-housed animals and it follows from this that, if conditions can be provided that preclude these factors, the risk of compromising animal welfare will be reduced. This means that we should provide conditions that give enough environmental challenge to be stimulating and yet not disturbing, and also provide opportunities to ensure that behaviour is not restricted.

So, how can this actually be achieved? Events throughout an animal's life affect its perception of stressors, but those that occur during its rearing, when it is young, have a particularly long-lasting and significant impact on its behavioural expression and development, as well as its perception of stressors. For example, domestic chickens reared in a complex outside environment show behavioural differences as adults when compared with

Figure 7.18 The so-called 'five freedoms' of animal welfare can be achieved by implementing best practice in terms of captive animal management. This is illustrated in the examples here: (a) freedom from thirst, hunger, and malnutrition is provided from a mother to her young calf; (b) freedom from discomfort is achieved by providing an appropriate environment for this pipefish (family Syngnathidae); (c) freedom from pain, injury, and disease is ensured by regular veterinary monitoring of this short-beaked echidna *Tachyglossus aculeatus*; (d) freedom from fear and distress is satisfied by allowing this maned wolf *Chrysocyon brachyurus* adequate space in which to distance itself from visitors; (e) freedom to express natural behaviours is stimulated through the provision of cognitive enrichment to these orang-utans *Pongo pygmaeus abelii*. (Photographs: (a), (c), and (d): Paignton Zoo Environmental Park; (b) Warsaw Zoo; (e) Moscow Zoo)

chickens reared inside. They show significantly less fear, as indicated by a shorter tonic immobility[11] righting time, and are also quicker to explore and use more of their outside environment (Grigor *et al.* 1995).

Similarly, deer mice *Peromyscus maniculatus* that are provided with enriched housing while they are young (less than 124 days old) display lower levels of stereotypy than those that are reared in standard housing. This effect persists into adulthood even if the mice are transferred into standard housing (Hadley *et al.* 2006). Therefore providing appropriate rearing conditions is essential in ensuring that an animal is able to interact effectively in its environment, and so has significant implications for the future life and success of animals (see also **section 9.5.1**).

Carlstead (1996) has suggested that captive environments are less complex, are more predictable, and afford captive animals less control than the native habitats in which they are adapted to live. Providing zoo animals with choices is a generally accepted method of giving them control in their environment. When giant pandas were given the choice to use different areas of their enclosure (inside and outside areas), their levels of both behavioural agitation and urinary cortisol decreased (Owen *et al.* 2005). Giving a similar kind of choice to polar bears *Ursus maritimus* led to a reduction in stereotypies and an increase in play behaviour (Ross 2006).

Another approach to minimizing the risks to welfare is to implement an evidence-based approach to zoo animal management (Melfi 2009; see also **Box 6.3**). As we have seen already in this chapter, good zoos are concerned not only with measuring welfare, but also with assessing whether or not current captive animal management represents best practice and whether change is necessary to promote better welfare. An evidence-based approach to welfare can be implemented by conducting a **welfare audit**, which is usually based on a review of the veterinary

and husbandry records for individual animals within a collection (for example, incidence of ill health or reproductive activity). Housing and husbandry parameters may also be recorded and reviewed to see whether there are common variables that are likely to affect welfare. Welfare audits, which aim to evaluate the welfare of all animals in the collection are a laudable goal, but have proved logistically impractical and so have not been widely adopted. However, implementing evidence-based animal management could provide a sustainable method of considering animal welfare for a large number of animals. There is a section on welfare audits in the *Zoos Expert Committee Handbook* (Defra 2012b). Other chapters and appendices within the *ZEC Handbook* provide useful examples of best practice within zoo housing and husbandry systems that have developed to ensure that welfare is not compromised,

7.5.3 Making choices

Unfortunately, even in the best zoos, animal welfare is likely to be compromised at some time during the animal's lifetime, whether as a direct result of housing and husbandry (for example, during catch-up of an animal for a health check), or indirectly (for example, if receiving injuries from conspecifics). There are also situations in which the zoo's goals and aims for a species might conflict with the welfare of the individual animals, such as conservation efforts that may require animals being moved between groups to ensure appropriate genetic management of the population.

In these situations, decisions need to be made on the basis of the relative 'costs and benefits' of the intended or current conditions in which an animal lives, and their impact on the animal's welfare. It is necessary, in these circumstances, to consider the costs and benefits not only to the individual animal, but also to the animals with which it shares an enclosure, and the animal's

---

[11] **Tonic immobility** is a natural state of paralysis that occurs in some species (fish, frogs, lizards, birds, rats, and rabbits) when they are threatened by an aversive stressor (see Maser and Gallup 1974).

captive population and species, as well as the impact for people. The currency used to consider these dilemmas can be highly variable, ranging from empirical indices of welfare to potential attitude changes in zoo visitors.

Another consideration that should be borne in mind when undertaking cost–benefit analyses is that the welfare of the animal and the impact of the 'topic under discussion' may vary over time. For example, informed discussion may decide that the short-term stress associated with moving an animal out of its natal group is outweighed by the costs incurred if it stays in the group and is injured as a result of fighting with the resident adults, or the benefits accrued from being able to breed in a new group.
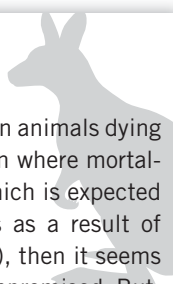
Life for animals in zoos, and in the wild, can be summarized as a complex series of events representing costs and benefits. For example, animals in zoos may be at greater risk of

---

Box 7.4   DOES A LONG LIFE EQUATE TO A GOOD LIFE?

The zoo profession has a tradition of celebrating births and long-lived animals in their populations, both internally where success in these areas is associated with professional expertise and recognized through professional awards, and also as the basis of many publicity and awareness campaigns. In the early days of zoos, survival of animals and births in the collection probably was something worth celebrating, given that these were rare events (see **Chapter 9**, 'Small population management'). Currently, there are some species whose natural history and captive management still perplexes us; however, for the most part, the expectation is that zoo animals should survive long enough to reproduce (if appropriate) and probably longer than this.

In **section 7.4.1** we discussed the contribution life history variables could make to our assessment of zoo animal welfare. Anecdotally, it would seem that the general rule that animals should survive and breed has been extrapolated to mean that those animals which live longest or have the greatest number of offspring have the best welfare. Whether this is a concept which is held within or outside the zoo profession, it is a factor which influences the captive management of animals, intentionally or not. There is some merit in the argument that animals that are able to breed may have better welfare than their barren conspecifics in terms of associated benefits of improved health and behavioural opportunities (see **section 9.5**). However, that long life equates to a good life has no sensible grounding in welfare science. If factors result in animals dying young, evidenced by a population where mortality doesn't correlate with age, which is expected in wild and captive populations as a result of senescence (Nussey *et al.* 2012), then it seems likely that welfare is probably compromised. But, it seems, misguided eagerness to maintain ever older animals is likely to result in greater welfare incursions due to pain and suffering in geriatric animals (Kitchener and Macdonald 2004). In **Chapter 6**, we explored the use of management euthanasia, where the lives of animals may be artificially curtailed to free up space for animals of greater conservation value, facilitate conservation goals, and support self-sustaining populations. In these instances, welfare is sometimes considered to be compromised because an animal has lived for a relatively shorter period of time, although if we compare longevity with the entire wild population, not just those individuals who have lived a long life, we are likely to find that zoo animals not only have a good quality of life, but also a longer life.

So how long a life is long enough? Long enough to breed, but short enough to avoid the deleterious effects associated with being a geriatric—maybe! This is a topic of constant debate within the zoo profession, littered with exceptions, caveats, advantages, and disadvantages, but nevertheless it is an important topic which requires consideration. And hopefully, in time some broadly agreed upon principles for best practice.

exposure to new diseases, but have access to veterinary care, and may have restricted control over their environment, social groupings, and proximity to people, but do not suffer from predation or starvation. Many more such examples could be given.

7.5.4 Ensuring best practice is implemented

Our increased understanding of animal welfare informs the legislative reform that is necessary to enforce the conditions that promote good animal welfare, but animal welfare legislation differs both between and within countries. For example, legislation is different in the USA, Germany, and Australia, but also between different states/territories within the USA, Germany, and Australia. This means that, in different countries, animals may or may not be protected by law (see **Chapter 3**). In the UK, for example, it is unacceptable to feed zoo animals live vertebrate prey unless there are 'extreme circumstances'[12], whereas the provision of live fish and other vertebrates is allowed and implemented in other countries (Defra 2004).

Summary

• Defining, assessing, and thus promoting good zoo animal welfare should be pursued as a scientific discipline.

• Approaches to welfare include the study of animals' minds, bodies, and natures, and by using analogy.

• Our current knowledge of zoo animal welfare is quite limited, because there is a large diversity of species held in zoos and our knowledge of their basic biology is sometimes lacking, making assessments of their welfare difficult.

• However, it is possible to identify needs in all animals and situations in which welfare may be compromised, and this enables zoos to work proactively to maintain high levels of animal welfare.

• Zoo professionals have a duty of care and thus are responsible for the welfare of the animals in their care, from when they are born to when they die.

• The continual monitoring of animals by trained and experienced staff is necessary to assess signs of poor welfare, which should then be swiftly followed by appropriate ameliorative action.

• Housing and husbandry conditions should exceed minimal standards, going beyond what is necessary to ensure an animal's survival, providing conditions under which an animal's behavioural and physical needs are met and a state of well-being can be attained.

Questions and topics for further discussion

1. Why should animal welfare be approached as a science?
2. What are the four approaches used to study animal welfare?
3. What factors are likely to compromise the welfare of zoo-housed animals?
4. Name some of the main indices used to measure animal welfare.
5. Can stress be considered beneficial?
6. What are the five freedoms?
7. How can zoos aim to maintain animals with good welfare?

---

[12] 'Extreme circumstances' are not frequently encountered, but may include cases such as the potential death of a highly endangered reptile because it will not eat, in which case it might be tempted to eat with live food.

Further reading

There are a number of good books that address the topic of animal welfare, but few of these are specific to the zoo industry and/or exotic animal welfare; instead, they are mainly biased towards farm, laboratory, or companion animals. However, the principles and theory of animal welfare are well portrayed, and a good general text that discusses factors that may compromise welfare is Appleby *et al.*'s *Animal Welfare* (2011). In addition, Kagan and Veasey's chapter on animal welfare in Kleiman *et al.*'s book, *Wild Mammals in Captivity: Principles and Techniques* (Kagan and Veasey 2010) and Dawkins's *Why Animals Matter* (2012) both provide easily accessible texts about animal welfare in a wider context. The Universities Federation for Animal Welfare (UFAW) also publishes a series of books on welfare topics, among which Fraser's *Understanding Animal Welfare* (2008) provides a great overview of the context in which animal welfare science is undertaken, and also a comprehensive overview of different animal welfare indices.

More specific texts, which deal in greater depth on topics within the field of animal welfare, include Mason and Rushen's *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare* (2006), Moberg and Mench's *The Biology of Animal Stress: Basic Principles and Implications for Animal Welfare* (2000), and Flecknell and Waterman-Pearson's *Pain Management in Animals* (2000).

Research undertaken to study the welfare of zoo animals can be found in the following journals: *Animal Welfare*, *Anthrozoos*, *Applied Animal Behaviour Science*, *Journal of Applied Animal Welfare Science*, and *Zoo Biology*.

Websites and other resources

To gain an insight into the field of animal welfare, it is necessary to use the published literature referenced above. However, there are a couple of websites that provide useful information about the practical implementation or assessment of animal welfare. The government website that details the legislation that governs practice in the UK can be found at **http://www.defra.gov.uk/food-farm/animals/welfare/**, and many of the regional zoo associations provide information detailing the expectations that they have of their member zoos, in terms of general animal management and welfare.

Finally, a website that you should all visit is **http://www.vet.ed.ac.uk/animalpain**, which provides brilliant and comprehensive coverage of animal pain.

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.
http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Chapter 8
Environmental enrichment

Anyone who visits **zoos** regularly, or reads some of the zoo literature, will be aware of the amount of effort that zoos make to stimulate their animals. This effort is generally referred to as **enrichment**. Enrichment is a broad concept, but the term is usually used to describe any change to an animal's environment that is implemented to improve the animal's physical fitness and mental well-being. The goals of enrichment are often to stimulate a wide variety of behaviours, and to improve the health and welfare of the target animal.

The methods used to provide enrichment are highly variable, but are often categorized and discussed by type: for example, 'food-related enrichment'. Unfortunately, the impact of providing enrichment cannot necessarily be generalized between species, or sometimes even individuals, and therefore a success in one situation might not translate well to another (Maple and Finlay 1989). That said, there are some changes that can be made to general housing and husbandry that reflect species-specific needs, and provide enrichment opportunities for zoo animals—for example, **scatter feeds** which have been incorporated into the husbandry of many animals, such as lion-tailed macaques (see Mallapur *et al.* 2007).

On the other hand, putative enrichments can be provided and yet no visible change observed. Spinelli and Markowitz (1985), for example, reported that changes in enclosure size and complexity had no significant effect on the behaviour of some laboratory- and zoo-housed primates. As such, it is necessary, if time is not available to test the efficacy of each putative enrichment provided, to use some 'rules of thumb' that will increase the likelihood that changes made to the animals' environments will be enriching (see **section 8.6**). There has been continued growth in the area of enrichment in recent years, with most zoos incorporating it into their housing and husbandry regimes and their education programmes for zoo visitors (**Fig. 8.1**).

In this chapter, we will cover the following topics.

- **8.1** **What is 'enrichment'?**
- **8.2** **The evolution of enrichment as a concept**
- **8.3** **The aims and goals of enrichment**
- **8.4** **Types of enrichment and their function**
- **8.5** **Enrichment evaluation**
- **8.6** **What makes enrichment effective?**
- **8.7** **The benefits of environmental enrichment**

The boxes that accompany this chapter examine some related issues, such as the relationship between enrichment and training and the organization of enrichment.

(a) No Lion' Around Here
To help George and Gracie keep active and alert, keepers installed a spring pull toy, with changeable scents and objects, like deer hides. It's so popular it's been broken twice!

(b) Why do we tease our animals?
We want our animals to live as natural a life as possible. That's why we sometimes hide their food, or make it difficult to get at. Hiding a monkey's food is not cruel and it's certainly not teasing either!
In the wild, fruit does not come neatly chopped into a bowl! Instead an animal has to search for it's meals. For an intelligent animal like a monkey, a lemur or a serval this searching can take up a large part of every day.
If we didn't hide our animals' food or we didn't allow them to hunt for their supper, we wouldn't be allowing them to behave naturally – and that would be cruel!

Figure 8.1 The implementation of enrichment provides an ideal opportunity to educate visitors about the needs of animals, and also to acknowledge sponsors and manufacturers of enrichment devices. Signs at zoos (a and b) explain to visitors why animals need enrichment and (c) acknowledge support from local companies. Often, the provision of enrichment is readily understood by zoo visitors, and provides a spectacle that will be viewed in a positive way, such as the provision of a ball for this lion at Howletts Zoo, UK (d). (Photographs: (a and b) Vicky Melfi; (c) Julian Doberski; (d) KNP/Howletts Zoo)

8.1 What is 'enrichment'?

There are many situations that might be termed 'enriching', and there is a tendency, in some zoos, to call all housing and husbandry changes 'enrichment'. But are they? Would you, for example, consider having an injection enriching? A vaccination may reduce the likelihood that an animal will contract a disease, and therefore improve its health and welfare, but do you think that this is comparable to a puzzle feeder, which would also confer benefits to the animal's overall well-being? These two methods both achieve improved well-being, through changes in housing and husbandry, which suggests that definitions of enrichment require clarity (Young 2003). Duncan and Olsson (2001) noted that enrichment should go further than alleviating poverty or meeting an animal's basic needs, but should also make the life of the animal richer.

Therefore it may be prudent to consider enrichment to be any change in an animal's life or environment that confers benefits beyond those necessary to fulfil the animal's basic needs; the five freedoms define an animal's basic needs (**section 7.5.1**). It is possible that 'stressful' events or challenges might lead to long-term benefits and be considered to be enriching, though this is an area of continued debate (as further discussed in **Chapter 7**).

8.2 The evolution of enrichment as a concept

The suggestion that enhancing the environments, and thus the lives, of captive animals could be beneficial was made by Hediger in the 1950s (Hediger 1950, 1955). But efforts to do this were not really focused until the work of Markowitz, who coined the term **behavioural engineering**, later known as **behavioural enrichment**. Markowitz suggested that behavioural enrichment could successfully stimulate desirable behaviours, increase activity, and provide an easy method of monitoring

health in zoo-housed animals (Markowitz *et al.* 1978; Markowitz 1982). In his work, animals were required to perform a task for which they would be rewarded—a method very similar to that employed in **positive reinforcement training (PRT)**.

Behavioural engineering is a technique based on **operant conditioning**, whereby the animal is required to express certain behaviours. Operant conditioning is the process whereby a behaviour is more likely to be repeated if it is followed by reinforcement, or less likely to be repeated if followed by punishment (as explained more fully in **section 4.1.2**).

Most of the tasks devised by Markowitz involved some kind of mechanical apparatus that could be set to deliver pre-loaded rewards whenever the 'goal' behaviour was performed (for example, touching a lever). Markowitz reported that behavioural enrichment led to the expression of desirable behaviours, because animals were motivated to work for rewards and thus would complete the task. For example, to achieve the aim of increasing activity levels in four Diana monkeys *Cercopithecus diana*, he provided them with a food reward after they had completed a complex series of movements around their enclosure (Markowitz *et al.* 1978). The monkeys quickly learnt that if they performed this series of behaviours, they would gain food, and so they became more active and were able to obtain more food rewards.

On the face of it, this approach seemed reasonably positive, but it received strong criticism at the time. The main objection was that the behaviour elicited in the animals was not 'natural'. It was considered that the behavioural expression resulting from behavioural engineering was artificial, and that the animals made no association between the behaviour they expressed and the environment (see **section 4.1.2**). This view was supported by the fact that goal behaviours resulting from behavioural enrichment were sometimes performed independent of environmental context, or at abnormally high levels (Hutchins *et al.* 1978). The rate of behavioural expression was determined by the reward

schedule determined by operant conditioning rules; the number and rate of rewards provided to animals after the successful completion of their task affects learning. So theoretically it would be possible to set the rate of reward to ensure that abnormally high rates of behaviour were not expressed (Forthman-Quick 1984).

A further criticism (Hutchins *et al.* 1978) of behavioural engineering was that the assertion that captive animals were motivated to work for rewards was **anthropomorphic**. We now know, however, that captive animals are frequently seen to work actively for a resource in their enclosure, even when it is also freely available (termed **contrafreeloading**; see **section 8.6.3**). Most of the arguments against behavioural enrichment were offered on the basis that an alternative, more naturalistic, enrichment approach was superior to this 'artificial' structuring of zoo animal behaviour.

This alternative, termed **environmental enrichment**, was suggested by Hutchins *et al.* (1978). They advocated that zoo animals should be provided with species-specific opportunities within their environments to enable them to express a diversity of desirable behaviours (**Fig. 8.2**). For example, to increase activity levels in the same group of Diana monkeys, the environmental enrichment approach would be to provide a large and complex enclosure. This would hopefully stimulate the monkeys to investigate and interact with their environment, and thus result in the desired elevated levels of activity. Therefore creating an environment with vegetation and structural complexity, referred to as a **naturalistic enclosure**, is integral to, although not mandatory for, the evolution of environmental enrichment, because it could provide a structural basis for daily enrichment (see **section 6.2.1**).

It is now clear that neither of these alternative styles is necessarily particularly natural, nor do they represent the panacea to providing an 'optimal' captive management system. For example, larger natural-looking enclosures do not necessarily lead to an elevation in activity levels (Spinelli and Markowitz 1985), and a feeding device may have limited impact on ameliorating stereotypical behaviour of zoo-housed bears (American black bears *Ursus americanus*) (see Carlstead and Seidensticker 1991; Carlstead *et al.* 1991). Support for the mechanistic approach of behavioural modification through behavioural enrichment has been overshadowed by the controversy that it has provoked and the overwhelming prejudice for the aesthetics associated with environmental enrichment. However, it is easy to appreciate how the two techniques can be employed to complement one another; for example, puzzle feeders can be provided in a large, dynamic, and complex enclosure. The two approaches are similar in their underlying mechanisms, but very different in their function (see **Box 8.1**).

Insights about enrichment theory and implementation are promulgated through publications and conference presentations, such as the International Conference of Environmental Enrichment (ICEE) which was first hosted by Metro Washington Park Zoo (now Oregon Zoo)
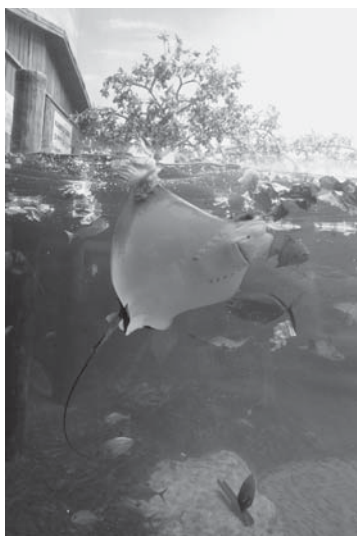
Figure 8.2 Providing animals with the opportunities to express natural behaviours may be as simple as providing enough water to allow social swimming, as seen in this mixed-species aquatic exhibit. (Photograph: Jeroen Stevens)

Figure 8.3 Providing environmental enrichment workshops has proved to be an effective method of transferring knowledge about good animal management. Here are examples of workshops hosted by (a) Beijing Zoo and (b) Edinburgh Zoo. (Photographs: (a) Kirsten Pullen, (b) Vicky Melfi)

in 1993 (Shepherdson 1998), the newsletter *Shape of Enrichment* edited by Karen Worley and Valerie Hare, and the recent development of Regional Environmental Enrichment Committees (REEC) which support a grass-roots approach to enrichment (the C in REEC is used to refer to committees or conferences synonymously). Capacity building for animal welfare, provided by Shape of Enrichment and other organizations, has the potential for making significant positive impacts on animal welfare (Melfi and Hosey 2011) (**Fig. 8.3**).

8.3 The aims and goals of enrichment

So, what should enrichment be trying to achieve? Most enrichment is implemented with the aim of generating some behavioural change in the target animal(s). That change may occur through the stimulation or prevention of specific behaviours that are associated with improved fitness and/or animal welfare. Many of these behaviours and the aims behind the provision of enrichment are interconnected. For example, frequently quoted aims of enrichment are to stimulate species-specific behaviour, to increase activity, and to prevent

stereotypies—for example, in giant pandas *Ailuropoda melanoleuca* (Liu *et al.* 2006).

We will consider each of these in more detail below, and they form a convenient summary of the behavioural aims of enrichment, as these are usually the focus of zoo studies. However, the positive ramifications of enrichment provision are more wide ranging than this, including improving physical development, spatial coordination, and reproduction—for example, in orange-winged Amazon parrots *Amazona amazonica* (Millam *et al.* 1995), bobcat *Lynx rufus* (Mollá *et al.* 2011), ratsnakes *Elaphe obsoleta* (Almli and Burghardt 2006), and gilthead seabream *Sparus aurata* (Batzina and Karakatouli 2012). Other benefits of enrichment are explored in **section 8.7**.

8.3.1 Wild-type behaviour

The goal of many enrichment studies is to promote wild-type, natural, or normal behaviours, and thus to bring captive and wild animal behaviours more in line with each other. Wild-type behaviours can be considered to be those that are expressed and observed in wild **conspecifics**. Definition of these terms, which are sometimes used synonymously with terms such as 'natural' or 'normal' behaviours, is rarely provided in studies and thus they become

meaningless. (Defining 'wild-type behaviour' and a discussion of the value of the concept is dealt with in **section 4.5**.)

Although it sounds very worthwhile and theoretically valid to promote wild-type behaviours as a goal for enrichment, in fact it is very difficult to achieve. Firstly, the premise of the wild–captive comparison is that deviations from the wild type indicate compromises in animal welfare. However, there are a number of theoretical and methodological reasons to suppose that this premise is not always correct (Veasey *et al.* 1996a) (see **section 4.5.2**).

Secondly, in order to promote wild-type behaviours in captive animals, a behavioural comparison of the wild and captive animals is necessary to establish whether there is a discrepancy and what it might be. An example of such a study is that by Kerridge (2005), who directly compared the behaviour of black-and-white ruffed lemurs *Varecia variegata* through observations of them in their native Madagascan rainforest habitat and in UK zoos (see **Box 4.5** for more on this study). But direct comparisons of this sort, through studying the species in both environments, are time-consuming and expensive, and require, at the very least, comprehensive knowledge of the wild animals' behavioural repertoire gained from the study of several representative groups of animals. Consequently, few have been undertaken. Thus there is a paucity of data for the many species held in zoos which would enable direct wild–captive comparisons to be performed.

An alternative has been to attempt a more symbolic comparison of wild and captive animal behavioural expression. This approach is characterized by the use of stereotyped assumptions of how captive and wild animal behaviours differ, rather than using actual data. For example, many captive animals are considered to be more inactive than their wild conspecifics and to display 'abnormal' behaviours (also discussed in **section 4.4**), often with little supporting evidence. Thus attempts are made to increase the captive animals' activity and to reduce any expression of 'abnormal' behaviour.

Although simple and widespread, this method of comparison is, unfortunately, too simplistic and may be based on erroneous ideas of what the animals are like in the wild. It may be true that some captive animals are more inactive than their wild conspecifics, but direct comparisons do not necessarily find significant differences in **activity budgets** between the two populations—in black-and-white ruffed lemurs, see Kerridge (2005), and in Sulawesi black-crested macaques *Macaca nigra*, see Melfi and Feistner (2002). So, at the very least, if approximation to the wild is what is being sought through enrichment, the intended behavioural profile should come from real data, not from guesswork. However, there is a good case for reducing **abnormal behaviour** where it is appropriate (see **section 4.4.3**).

8.3.2 Desirable versus undesirable behaviours

The promotion of wild-type behaviour is sometimes used as a euphemism for promoting desirable and inhibiting undesirable behaviours. Clearly, we need to consider very carefully which behaviours are assigned to which category, because their stimulation or prevention may have far-reaching ramifications. Many enrichment studies, for example, aim to promote feeding and **foraging**, and to ameliorate abnormal behaviours, i.e. stereotypies and **self-injurious behaviours**—in the fishing cat *Prionailurus viverrinus*, see Shepherdson *et al.* (1993), and in the chimpanzee *Pan troglodytes*, see Baker (1997). But why should we think that feeding and foraging are desirable behaviours to be increased? Unless a direct comparison of time spent feeding and foraging has been performed, how do we know how much time the animals should spend performing these behaviours?

Similarly, it is possible that the expression of some behaviours, i.e. stereotypies or **self-directed displacement behaviours** provides the animal with a coping mechanism for living within a challenging environment (see **section 4.4**). If this is the case, then what does their reduction mean for the welfare of the animal?

8.3.3 Activity versus behavioural diversity

The drive to generate greater activity in captive animals is extremely strong, even though direct comparisons of the activity levels of wild and captive animals are rarely performed. For example, wild lions spend many hours resting and yet enrichments have been designed to promote activity in this species when in captivity (Powell 1995). Part of this drive is almost certainly led by zoo visitors, who wish to see active animals (**Fig. 8.4**)

Figure 8.4 It is easy to see why visitors may want to see active animals: the running (a) sloth bear *Melursus ursinus* at Wroclaw Zoo and (b) cheetah *Acinonyx jubatus* at Vienna Zoo both look more interesting than the (c) lion *Panthera leo* and (d) the guenon species also pictured. (Photographs: (a) Radaslav Rata/Wrocław Zoo; (b) Vienna Zoo; (c) Andrew Bowkett; (d) Vicky Melfi)

(see **section 6.1.3**). Certainly, many believe that environmental differences between captivity and the wild are likely to lead to quantitative changes (changes in the amount) in animal behaviour (Carlstead 1996).

Quantitative assessment of behaviours can be made through the generation of activity budgets, which describe the amount of time that the animal spends performing different behaviours, usually in a day (there is more about activity budgets in **section 14.4.1**). But it is not only between wild and captive populations that environmental variation exists, but also within wild and captive populations (Hosey 2005). For example, variation in activity budgets was higher between three wild Sulawesi macaque groups compared with eight captive groups (Melfi 2001) (**Fig. 8.5**). This might mean that activity budgets are not sensitive enough to detect small differences between different groups of animals, but may also suggest that behaviour is sufficiently flexible that the slight differences seen between different captive conditions are not particularly important. Perhaps what is important is whether they fall within the range of variation seen in wild populations.

Qualitative differences in behaviours (type of behaviour) may also occur as a result of environmental differences between wild and captive populations, so there may be behaviours shown in the wild, but not in captivity, and vice versa. There can

be practical limitations to comparing specific behaviours between wild and captive situations. As an alternative **behavioural diversity** (the number of behaviours that an animal expresses) can provide an indication of how wild and captive behaviours compare qualitatively.

It has long been feared that animals in captivity may not be able to express certain behaviours and may even lose them over time (Frankham *et al.* 1986). Of particular concern would be the loss of behaviours that are necessary for the animal to survive in the wild (see **section 9.2.4**). The loss of these behaviours would seriously impede long-term conservation efforts, because the animals would no longer have the skills for surviving in the wild (Box 1991). For example, Britt (1998) observed that black-and-white ruffed lemurs gained much of their food in the wild by suspending themselves upside-down by their feet, and using their hands and mouths to gather up the food. But he also observed that this method of feeding was not usually possible in captivity because many animals were fed on the ground from dishes. Thus, an appropriate enrichment for the lemurs would be one that encouraged the diversity of feeding postures and behaviours seen in the wild.

Some behaviours are performed infrequently or for short durations, but expressing these behaviours may still be very important to the welfare of animals. For example, farmed mink *Mustela vison*
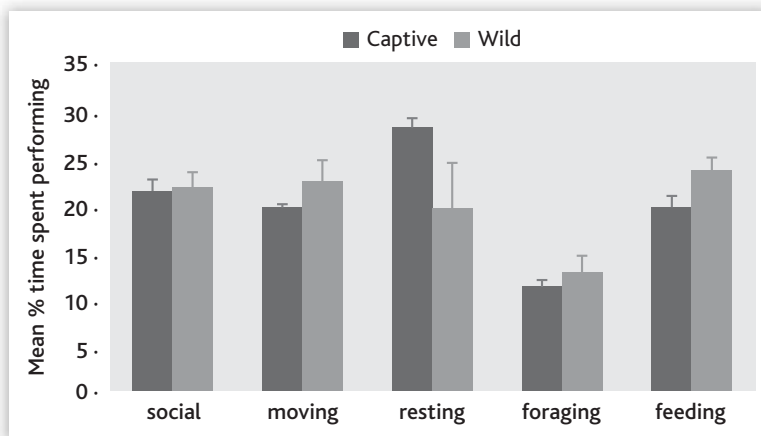
Figure 8.5 Despite the general assumption that wild and captive animals will behave differently, a comparison of activity budgets constructed for captive ($N = 8$) and wild ($N = 3$) Sulawesi crested black macaques found that they were not significantly different. (From Melfi 2001)

have demonstrated that they will push very heavy weights to gain access to water for swimming, even though this behaviour did not occupy much of the activity budget of the animals (Mason *et al.* 2001). So, the ability to perform all of the different kinds of behaviour that are in the animals' repertoire is clearly of importance to them and enrichment can be designed to promote these behaviours. An additional benefit is that observing animals perform their species-specific behaviour is important in public education and in promoting positive attitudes towards zoos (Forthman *et al.* 1992). Thus, the promotion of behavioural diversity or species-specific behaviours may be a more suitable goal for enrichment than simply increasing activity levels.

8.4 Types of enrichment and their function

Enrichment comes in many shapes and forms. Categorizing enrichment into meaningful groups can help with its practical provisioning and can also give an indication of the enrichment's function by acting as a kind of 'rough guide' to its expected outcome. For example, food-based enrichments would probably be expected to promote feeding and foraging behaviours. Much enrichment will affect animals in a variety of ways, however, so it can be difficult to assign a category for an enrichment, because it might seem to fit into more than one. A puzzle feeder, for example, can be manipulated and therefore could be thought of as a physical, or even a cognitive, enrichment, but it delivers food so is also food-based.

We can suggest the following as enrichment categories (**Fig. 8.6**).

1. *Food-based enrichment*: these centre on food (for example, providing food in a new way or providing a new type of food).

2. *Physical enrichment*: any change to the animal's structural environment, whether permanent or temporary (for example, perching or climbing frames), or the provision of objects that can be manipulated (for example, flooring substrates or toys).

3. *Sensory enrichment*: anything that stimulates the animal's senses, including what it sees, hears, and smells (for example, light reflecting off hanging crystals, a rattle, or blood trails).

4. *Social enrichment*: interactions with other animals or people.

5. *Cognitive enrichment*: additions to the environment that require problem solving of differing degrees of complexity to stimulate the animal mentally. Meehan and Mench (2007) suggested that animals' cognitive skills could be challenged by requiring them to use '*navigational, tool-making or cooperative social skills*' within their daily lives.

8.4.1 Food-based enrichment

Many species have evolved to spend a large proportion of their day looking for, processing, or eating food. Captive environments may offer few opportunities for foraging or feeding, and the food provided frequently requires little processing[1] by the animal, because it has already been processed by keepers.

Some studies have demonstrated that captive animals can spend less time in food-related behaviours and/or express a lower diversity of food-related behaviours than their wild counterparts. To this end, many feeding enrichments aim to prolong the feeding experience by making the acquisition of food more difficult (for example, by hiding the food, or making it hard to obtain in a puzzle), or by providing food that is low in calories so that, once found, more food needs to be eaten. The provision of food highly motivates animals, so they are more likely to use the

---

[1] **Processing** is a term often applied to the activities that an animal performs to gain access to food (e.g. manipulating food and choosing which parts to eat) and does not necessarily include ingestion.
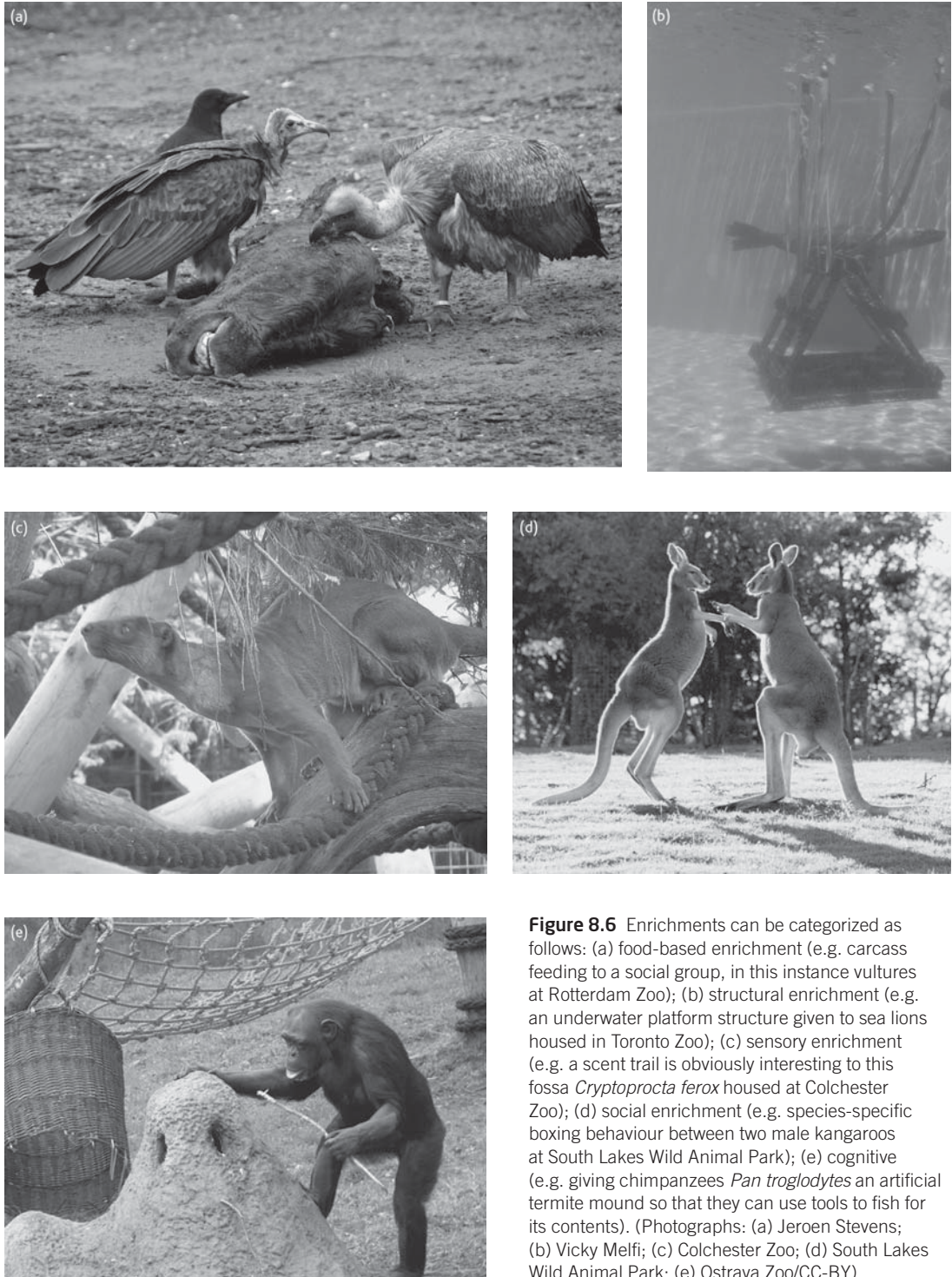
Figure 8.6 Enrichments can be categorized as follows: (a) food-based enrichment (e.g. carcass feeding to a social group, in this instance vultures at Rotterdam Zoo); (b) structural enrichment (e.g. an underwater platform structure given to sea lions housed in Toronto Zoo); (c) sensory enrichment (e.g. a scent trail is obviously interesting to this fossa *Cryptoprocta ferox* housed at Colchester Zoo); (d) social enrichment (e.g. species-specific boxing behaviour between two male kangaroos at South Lakes Wild Animal Park); (e) cognitive (e.g. giving chimpanzees *Pan troglodytes* an artificial termite mound so that they can use tools to fish for its contents). (Photographs: (a) Jeroen Stevens; (b) Vicky Melfi; (c) Colchester Zoo; (d) South Lakes Wild Animal Park; (e) Ostrava Zoo/CC-BY)

enrichment; as such, it is not surprising that food-based enrichment is the easiest and most abundant type provided.

Foraging can be stimulated simply by hiding food in flooring substrates, a method that has been shown to increase enclosure use, activity, and behavioural diversity, while decreasing the incidence of aggression and abnormal behaviours: in chimpanzees, see Baker (1997); in rhesus macaques *Macaca mulatta*, see Lutz and Novak (1995); in white-faced capuchins *Cebus capucinus* see Ludes-Fraulob and Anderson (1999). Additional surface areas for foraging can be provided, in the form of foraging boards: in rhesus macaques, see Lutz and Novak (1995); in the squirrel monkey *Saimiri sciureus*, see Fekete *et al.* (2000). The use of flooring substrates may change over the course of the day, according to the animals' motivation. Guinea pigs *Cavia porcellus* were found to prefer wood shavings during the day, when they would rest in them, but then prefer cut paper at night time (Kawakami *et al.* 2003). Food can also be hidden in log piles, which have been shown to increase significantly the amount of time that bush dogs *Speothos venaticus* spend exploring their enclosure (Ings *et al.* 1997b). It was suggested that the bush dogs learned to be more proficient in searching and finding food with repeated use of the log pile, which was observed as a significant decline in searching behaviour with time (**Fig. 8.7**).

The Equiball™, designed for stabled horses, also increases the processing time required to gain access to food and has been shown to reduce stereotypies in horses *Equus caballus* (Henderson and Waran 2001) (**Fig. 8.8**). The Equiball™ can be set to release high-calorific food concentrates slowly when it is 'nudged' along the ground by the horse. This has two benefits: it increases the time required to feed and also encourages more movement. Similar feed balls designed in all shapes, sizes, and materials are available for a wide variety of animals, and they have also been fixed above ground for arboreal species which need to use dexterity to gain access to the food.

Food can also be presented in such a way that species-specific behaviours are required to obtain it. The inability of ruffed lemurs to express all their different feeding postures when they are only fed chopped fruit on the ground was mentioned in the previous section. To promote these postures in zoo lemurs, Britt (1998) provisioned them from the roof of their enclosure and also by using suspended feeding baskets. These enrichments encouraged the lemurs to use the vertical space of their enclosure and to gain food as they would in the wild, using suspensory feeding postures. Indeed, the lemurs were observed to spend as much of their feeding time using suspensory feeding postures when these enrichments were used as did their wild
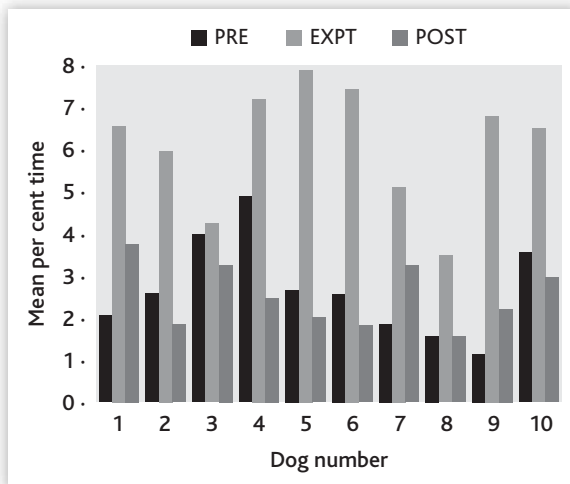
Figure 8.7 Food hidden in a log pile for bush dogs *Speothos venaticus* at Edinburgh Zoo significantly increased the time that they spent searching for food. The mean percentage time that the bush dogs spent foraging for food increased from 2.7 per cent of observations, with 'normal' feeding conditions (before (PRE) and after (POST)), to 6.1 per cent when the log pile was used (EXPT). (From Ings *et al.* 1997b)
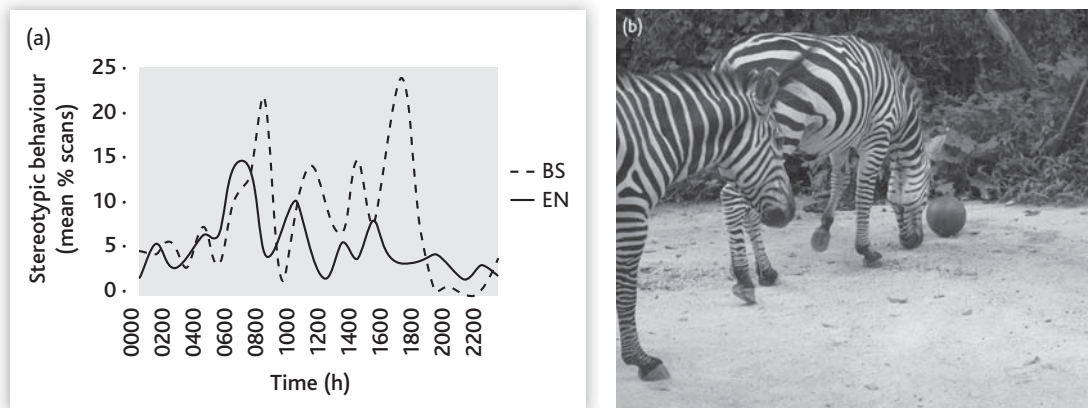
Figure 8.8 (a) Prior to provisioning with the Equiball™ (BS), six stabled horses were observed to spend 5.27 ± 8.17 per cent of their time performing stereotypies, which peaked during two feeding periods at about 08.00 and 17.00. When the Equiball™ was used (EN), stereotypies were reduced in five out of the six horses. This highlights how individuals may differ in their acceptance of changes to housing and husbandry. (b) A variety of feeding balls can be provided to zoo animals, as seen here provided to zebra *Equus burchellii* in Singapore Zoo. ((a) From Henderson and Waran 2001; (b) Photograph: Low Ai Ping/Singapore Zoo)

equivalents (wild, 25 per cent; rooftop, 24 per cent; suspended baskets, 30 per cent; standard and scatter feed, 5 per cent).

Providing food unpredictably has also been considered enriching. It has been suggested that pre-feeding anticipation (PFA), also termed food anticipatory activity (FAA),[2] is one of the main contributory factors influencing the development of stereotypies (Howell *et al*. 1993; reviewed by Mistlberger 1994) (see **Chapter 7**). So it has been reasoned that, if food presentation is less predictable, the development of PFA may also be hindered. Certainly, the amount of time that white-fronted brown lemurs *Eulemur albifrons* and Alaotran gentle lemurs *Hapalemur alaotrensis* at Zurich Zoo spent active and moving increased when they were provided with food boxes which would open randomly, providing food (Sommerfeld *et al*. 2006). Similarly, a mealworm feeder that randomly dispensed food to a group of Rodrigues fruit bats *Pteropus rodricensis* led to a significant increase in activity and a decline in aggression, even in bats that were not observed to use the feeder (O'Connor 2000) (**Fig. 8.9**). In

cheetahs *Acinonyx jubatus* at Fota Wildlife Park, randomizing the timing and location of food led to an increase in exploratory behaviour and a decrease in pacing (Quirke and O'Riordan 2011). It has been proposed by Watters (2009) that optimal foraging theory (see **section 4.1.4**) suggests that food presentation should be temporally variable, and when this was done with fennec foxes *Vulpes zerda* the animals showed increased behavioural diversity and activity (Watters *et al*. 2011).

Various methods have been used to reduce the predictability of food availability to zoo-housed animals. For example, a hollowed-out coconut was used at the Bronx Zoo to distribute live food (insects) randomly to **dendrobatid frogs** which led to an observed increase in activity (Hurme *et al*. 2003).

With so much emphasis placed on food as the motivator for enrichment, care should be taken that the provision of enrichment does not indirectly lead to more food (calories) being provided than is necessary to meet the animal's daily requirement, because this might result in obesity. As a rule, any food-based enrichment should use food from the animal's daily ration. Providing

[2] **Pre-feeding anticipation (PFA)**, or **food anticipatory activity (FAA)**, is the behavioural expression observed prior to being given food, which can occur due to a variety of signals, including circadian, visual, or odour.
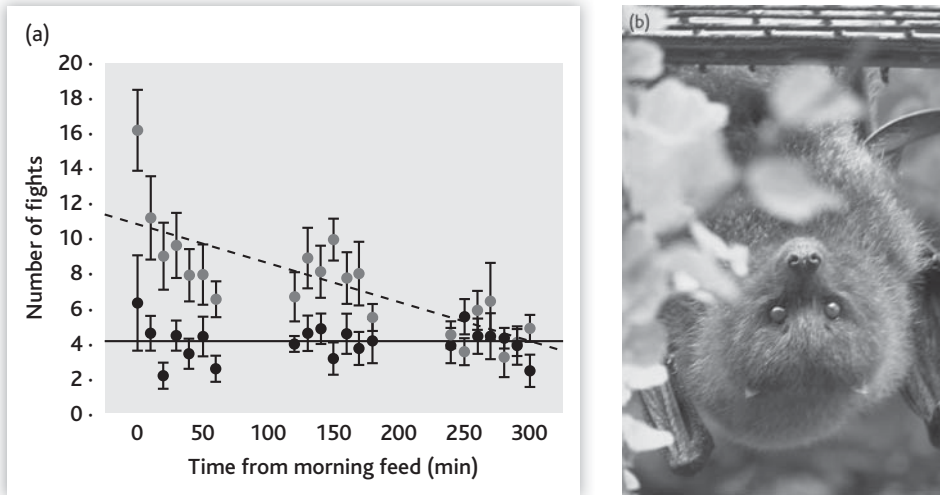
Figure 8.9 The number (mean $\pm$ SEM) of fights that occurred between Rodrigues fruit bats *Pteropus rodricensis* declined over time after their morning feed when no enrichment was present (grey circles). When mealworms were present in the dispenser (black circles), the number of fights that occurred remained low, regardless of feeding time. ((a) From O'Connor 2000; (b) Photograph: Paignton Zoo Environmental Park)

food that is low in calories can be an option if more food is necessary for the enrichment than would normally be given. This mirrors what, in fact, happens for many wild species—that is, that they spend long periods of time feeding, because the food they are eating is of low nutritional quality (see **Chapter 12**). This means that a more 'naturalistic' way of feeding would be to provide fresh foods, which are not as nutritionally rich as many concentrates (manufactured food). For example, provision of browse increased activity levels in African elephants *Loxodonta africana* (Stoinski *et al*. 2000) and Livingstone's fruit bats *Pteropus livingstonii* (Masefield 1999) (see **Box 12.1** for further information about feeding browse to zoo animals). Similarly, carcass feeding has been associated with many behavioural benefits in zoo-housed **Carnivores** (**Box 12.6**).

Some species may have specialized feeding requirements, such that they have anatomical adaptations to deal with certain foods. For example, the diet of wild common marmosets, like other marmosets, includes gum exudates from trees, for which they have a specially developed tooth comb designed to aid in the gouging out of gum from trees (**Fig. 8.10**). Gum feeders were initially

used by McGrew *et al*. (1986); later, Roberts *et al*. (1999) showed that, in laboratory housed common marmosets *Callithrix jacchus*, gum feeders reduced the time spent in stereotypical pacing and sitting. However, their use of the device declined over time, as did observed changes in their behaviour, towards the end of a 3-hour exposure to the device and after about three days, when the device was provided daily.

Figure 8.10 Providing gum feeders, filled with acacia gum, to pygmy marmosets *Cebuella pygmaea*, as seen here, enables them to display species-specific feeding behaviours. (Photograph: Paignton Zoo Environmental Park)
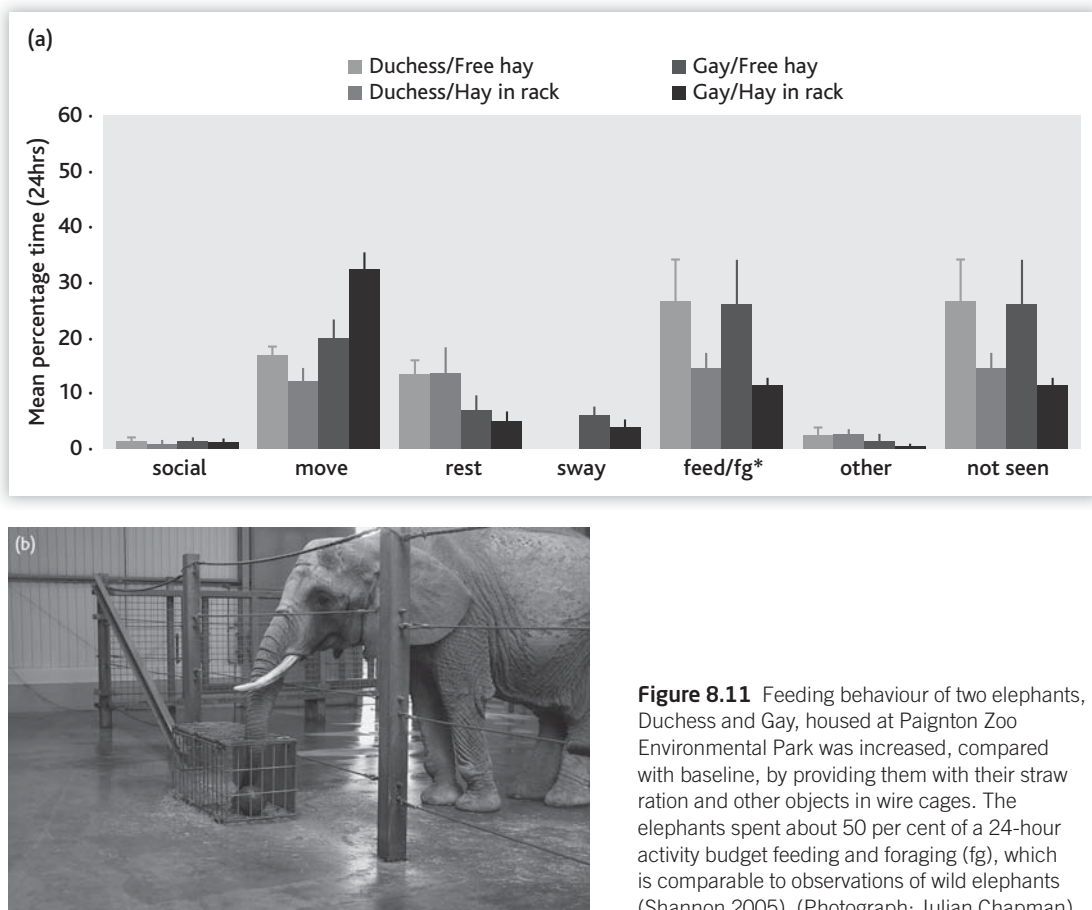
Figure 8.11 Feeding behaviour of two elephants, Duchess and Gay, housed at Paignton Zoo Environmental Park was increased, compared with baseline, by providing them with their straw ration and other objects in wire cages. The elephants spent about 50 per cent of a 24-hour activity budget feeding and foraging (fg), which is comparable to observations of wild elephants (Shannon 2005). (Photograph: Julian Chapman)

At Paignton Zoo Environmental Park, straw was provided in wire racks to two elephants (Melfi *et al.* 2004a). This not only provided food of low nutritional quality, but in a device that required the elephants to use their highly dextrous manipulative trunks to gain food. Providing straw daily in these wire mesh cages maintained a high level of feeding and foraging in these two captive elephants, as illustrated in **Fig. 8.11**.

8.4.2 Physical enrichment

Good enclosure design incorporates structural enrichment through the inclusion of beams, platforms, ponds, and anchors for fixing perching and objects, as illustrated in **Fig. 8.12**. Many of these features are permanent, but many of them can be modified with some imagination or moved to provide animals with a different perspective. For example, a pond can be filled with water or different substrates, and small bits of food can be provisioned in either the water or the substrates (e.g. Robins and Waitt 2011). In addition, perching, and the use of ropes, beams, and branches, can be rearranged or renewed within an enclosure and this can essentially 'rejuvenate' the exhibit. For example, providing climbing structures within a spectacled bear *Tremarctos ornatus* exhibit at Philadelphia Zoo increased the bears' behavioural diversity and use of the enclosure (Renner and Lussier 2002).

It is well known from laboratory studies that some species show a need for privacy. For example, laboratory-housed rabbits provided with a sheltered area as part of an enriched cage system displayed lower levels of restlessness, grooming,

Figure 8.12 The enclosures at (a and c) the Smithsonian's National Zoo and (b) Disney's Animal Kingdom are both good examples of how structures can be provided that enable animals, here orang-utans *Pongo pygmaeus* and siamangs *Hylobates syndactylus*, respectively, to use species-specific locomotion skills to travel great distances. (Photographs: (a) Mehgan Murphy/Smithsonian's National Zoo; (b) Julian Chapman; (c) Jessie Cohen/Smithsonian's National Zoo)

bar-chewing, and timidity, and this was especially true of females compared with males (Hansen and Berthelsen 2000). Many zoo animals have a similar need for privacy and this can be provided by increasing the amount of cover in the enclosure. Leopard cats *Felis bengalensis* at the National Zoo in Washington were observed to lie in hiding places within their enclosure when their urinary **cortisol** levels were high, indicating that when they were stressed, they would seek
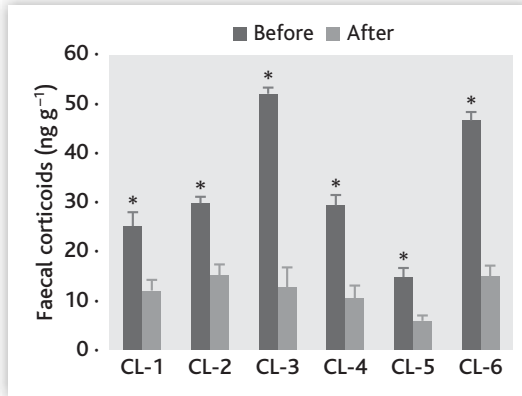
Figure 8.13 Hiding spaces are important to clouded leopards *Neofelis nebulosa*. Prior to the provision of hiding places (before), six leopards all showed some level of behavioural pathology, which was associated with high levels of faecal cortisol. When hiding places were provided within their enclosure (after), there was a significant decline in the faecal cortisol measure in each leopard. (From Shepherdson *et al.* 2004)

out privacy (Carlstead *et al.* 1993). When hiding places, as well as perching, were provided, the cats showed increased exploratory and decreased stereotypical behaviours relative to those seen in their previously unenriched enclosures. This is further supported by the finding that, when hiding places were provided for clouded leopards *Neofelis nebulosa*, their faecal cortisol levels declined significantly (Shepherdson 1994) (**Fig. 8.13**).

Other species also appear to need a large degree of cover. For example, Chamove (1989) described how groups of common marmosets and cotton-top tamarins *Saguinus oedipus* avoided areas without cover and thus did not use a large open area, although this provided additional space. However, when dense cover was provided, their use of the area became extensive.

Visual barriers have been used to provide privacy or protective areas within an enclosure. When large groups of domestic fowl (*N* = 80 and 110) had vertical panels installed in their enclosure, the time that they spent resting increased significantly, whereas foraging declined significantly, although feeding itself was not affected (Cornetto and Estevez 2001). However, provision of barriers appears to have

mixed results, depending on the species' natural history. Thus, for example, the ability to escape visually from other group members reduces aggressive encounters in stump-tailed macaques *Macaca arctoides* (Estep and Baker 1991), but increases aggression in pig-tailed macaques *Macaca nemestrina* (Erwin 1979). Both of these primate groups were maintained as single-male multi-female troops, but the source of aggression (and thus social tension) was different in the two groups. In the pig-tailed macaque group, the males interrupted female–female aggression, and so an increase in aggression was observed when cover was provided because the male was unable to see all the females and this prevented him from breaking up aggression between them. However, in the stump-tailed macaque group, the male usually initiated male–female aggression, so the visual barriers reduced social tension and aggression because the females were able to hide from him.

Qualitative features of the perching can also affect behaviour. Caine and O'Boyle (1992) demonstrated that the orientation of perching in an enclosure for red-bellied tamarins *Saguinus labiatus* affected the type and duration of time spent playing. Vertical substrates stimulated more chasing and grasping behaviours through the expression of a greater variety of play sequences compared with behaviours observed on horizontal substrates.

Objects are frequently used as enrichments. Zimmerman *et al.* (2012) demonstrated that enrichment could be used as part of a programme to deter Atlantic cod *Gadus morhua* from biting through their net cages. Objects provided included PVC pipes, a tennis ball attached to rope (cod are attracted to fraying rope), and a knobbly rubber ball; this study found that 97 per cent of enrichment interactions were with the PVC pipe. Other simple, but effective, objects have included ice blocks, which significantly increased behavioural diversity in African dwarf crocodiles *Osteolaemus tetraspis*, representing greater interaction with, and use of, their environment (Melfi *et al.* in prep.). The type and shape of object enrichments
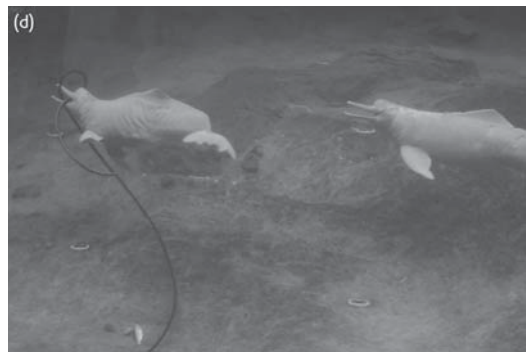
Figure 8.14 Junk? Many objects that may otherwise be discarded can easily be transformed into enrichment objects. Here you can see that 'spent' film canisters have been made into a variety of mealworm dispensers for (a) Goeldi's monkeys *Callimico goeldii* and (b) meerkats *Suricata suricatta* at Paignton Zoo Environmental Park; (c) old banana boxes with mongoose *Mungos mungo*; (d) a hose is provided to pink river dolphins *Inia geoffrensis* in Duisburg Zoo. (Photographs: (a) and (b) Julian Chapman; (c) Jeroen Stevens; (d) Vicky Melfi)

are endless, including unwanted items that would otherwise be thought of as 'junk', such as old film canisters and cardboard tubes used as mealworm feeders or a method for delivering scents, as shown in **Fig. 8.14** (Fry and Dobbs 2005).

8.4.3 Sensory enrichment

Because we are such 'highly visual' animals ourselves, we can frequently forget that other animals gain information about their environment using many different modalities as well as, or instead of, vision. Visual, olfactory, and auditory channels are all important means of communication for animals, and are routes of information that we are able to manipulate within a zoo environment; we can also modify the tactile information available. With some imagination, it is also possible to affect thermal, humidity, and electromagnetic gradients, and the tastes available to captive animals.

For example, we can provide thermogradients for Round Island geckos *Phelsuma guentheri* (Wheler and Fa 1995) and artificial algae for dolphins *Tursiops truncatus* (Edberg 2004), and can meet all four senses of **elasmobranchs** which include vision, chemoreception (including smell and taste), mechanoreception (hearing and touch), and electroreception (Smith 2006).

Despite the fact that many zoos use sensory enrichment, described in many *Shape of Enrichment* articles (see **section 8.2**), few of these enrichments have been tested empirically. Some reasons and resolutions to providing scent and auditory enrichment are given by Clark and King (2008) and by Farmer and Melfi (2008), and a review of the effectiveness of sensory enrichment is given by Wells (2009).

An example of sensory enrichment is the use of computer-controlled acoustic information in the form of bird sounds (Markowitz *et al.* 1995). Bird noises played randomly in the enclosure of a leopard cat *Prionailurus bengalensis* signified that food could be found. Towards the end of this study, the leopard cat had learnt that foraging in association with this noise could lead to food rewards. Black-footed cats *Felis nigripes* at Belfast Zoo were provided with cloths impregnated with one of two artificial odours (nutmeg and catnip) or the body odour of a quail, a prey species (Wells and Egli 2004). All the odours increased the activity of the cats, although nutmeg had less impact than catnip or the prey species odour.

Television has also been used as a means of visual enrichment. Bloomsmith and Lambeth (2000) provided laboratory-housed chimpanzees with a variety of videotapes showing different scenes (chimpanzees, other animals, and humans). Not surprisingly, single-housed chimpanzees watched the television more than those that were socially housed, although there was a lot of individual variation. Similarly, gorillas preferred to watch videotapes of other gorillas than tapes of humans, and particularly liked watching mixed-sex groups

engaged in agonistic behaviour, which thankfully did not increase their own aggression (Maloney *et al.* 2011).

Care needs to be taken when providing sensory enrichment, because you may not always be aware what information you are communicating to your animals. This uncertainty can be reduced by ensuring that you know in what context the information was gained. For example, when playing back vocalizations (playbacks),[3] do you know what messages you are sending? O'Brien (2006) used playbacks of conspecific vocalizations with Toco toucans *Ramphastos toco* at Dublin Zoo, but found that they had limited positive impacts on the birds' behaviour. The male bird was observed to feed less during playback conditions compared with baseline days, which was suggested to be a sign of stress.

Equally, when providing olfactory information, it is important to know the relationship between the target animal and the animal responsible for the sample (predator or prey). Buchanan-Smith *et al.* (1993) demonstrated that cotton-top tamarins expressed behaviours associated with anxiety when presented with predator scents. Similar results have also been observed in prey species that are able to see predators. Stanley and Aspey (1984) observed that five African **ungulates** spent less time expressing several different behaviours (lying down, feeding, drinking, sniffing the ground and each other) when an African lion was visible (there is more about both of these studies in **section 4.3.2**).

In terms of biological samples (for example, faeces, urine, and shed skin) used for sensory enrichment, it is necessary to ensure that all samples are from known healthy animals and do not provide a route for the transmission of disease.

8.4.4 Social enrichment

Possible sources of social enrichment are provided by people or other animals (for example,

---

[3] Studies that play sounds—whether vocalizations, music, or other noises—to animals are often referred to as **playback experiments**, which is sometimes shortened and described simply as **playbacks**.

Figure 8.15 Appropriate social housing can be a good source of dynamic enrichment; for example, (a) this pair of marbled polecats *Vormela peregusna* at Novosibirsk Zoo, or (b) the pair of dragons *Pogona henrylawsoni*. (Photographs: (a) Novosibirsk Zoo; (b) Jessica Goldman)

Fig. 8.15); a framework to explore the potential for humans to act as enrichment has been reported by Claxton (2011) and this topic is discussed further in **Chapter 13**. Sometimes, the presence of other species in **mixed-species exhibits** might also be enriching (see **section 6.3.3**). In this section, we consider how conspecific social groups may function as enrichment.

Cage-mates are the most obvious source of social interaction, whether of the same, or a different, species. Indeed, cage-mates provide dynamic and unpredictable sources of stimulation, which may be one of the most enduring and effective ways of delivering enrichment to captive animals. Most of the evidence for this comes from laboratory studies, probably because it is becoming increasingly unusual for zoo animals to be housed in anything other than social groups. But in the laboratory industry, where animals are routinely housed singly, there is much evidence demonstrating the importance of social housing (Eaton *et al.* 1994). For example, Reinhardt and Reinhardt (2000) argue that social enrichment is essential for captive primate welfare and many studies have shown that, even in very small cages, the provision of a cage-mate can be of great benefit (Reinhardt 1994a; 1995; Reinhardt *et al.* 1998).

In extremely restricted environments, social enrichment has been shown to reduce stereotypies when other environmental changes (such as objects and devices) have failed (Spring *et al.* 1997). Schapiro *et al.* (1997) have suggested that social housing could improve the effectiveness of object enrichment, but social pressures can equally complicate the use of object enrichments because of the monopolization of resources, resulting in aggression.

Some species which are thought to be solitary in the wild are kept in social groups in captivity. For example, tigers are often pair-housed in zoos. In a comprehensive review of enrichment provided to zoo-housed tigers, Szokalski *et al.* (2012a) noted that little was known about the potential for social enrichment, although it would seem from data collected by De Rouck *et al.* (2005) that housing tigers *Panthera tigris* in pairs is advantageous, because the animals are then able to perform a greater diversity of behaviours compared with tigers housed alone. Despite the overwhelming benefits of social housing, there are inherent difficulties in managing it, because it can be associated with a myriad of pressures that can result in stress, physical injury, and disease (Visalberghi and Anderson 1993). Nevertheless, because social housing is the 'norm' within zoos, housing and husbandry regimes have evolved to reduce any deleterious side effects that may occur (see **Chapter 6**).

8.4.5 Cognitive enrichment

Some kinds of enrichment work by providing captive animals with mental stimulation, such as working out a complicated route to food. Indeed, much has been learnt about the cognitive abilities of a wide array of species by providing them with this sort of enrichment. For example, offering different cognitive tasks to Eastern black-and-white colobus monkeys *Colobus guereza kikuyensis* led to different animals developing different behavioural traditions (Price and Caldwell 2007). Enrichment devices are seldom the only source of food available; generally, other sources of food are available in the enclosure concurrently, or else regular meals will ensure that the animal does not 'need' to use the enrichment.

So, if food is available anyway, why do animals choose the cognitively demanding task? This phenomenon of contrafreeloading is discussed more fully in **section 8.6.3**.

An example of cognitive enrichment is a puzzle feeder which requires dexterity (using hands, beaks, or trunks) to manipulate, and which has been used with a variety of animals. The observation that some animals use tools to gain access to food has also led to the development of more complicated enrichment tasks. For example, some primate and bird species have been observed using tools to crack nuts. In an attempt to make the use of a tool to crack nuts even more necessary, Visalberghi and Vitale (1990) coated provisioned nuts with a paste made of sawdust and non-toxic glue to make them harder, and thus more difficult for tufted capuchins *Cebus apella* to open. Using food in cognitive enrichment tasks not only increases the likelihood of the device being used, but also requires species-specific behaviours to be expressed to gain the food and prolongs the time spent by the animal in attempting to access the food object.

Some zoos have created purpose-built facilities for research into animal **cognition**. In 2001, Germany's Leipzig Zoo heralded the opening of the Wolfgang Köhler Primate Research Center, which serves as a state-of-the-art zoo enclosure and also maintains animals that are the subject of high-quality research (Pennisi 2001). Edinburgh Zoo in Scotland is home to the 'Living Links' Centre, which fulfils similar functions (see **section 14.3.5**).

8.5 Enrichment evaluation

Some previous studies have noted situations in which enrichment has apparently not worked (Hare 2008; Rosier and Langkilde 2011). In cases such as these, it is more accurate to consider that the changes made to the life or environment of the subject were not enriching, and therefore not that the enrichment has failed, but that the change provided does not constitute enrichment. Therefore it is essential that all changes made potentially to enrich animals are undertaken with expected outcomes in mind.

To evaluate the effectiveness of a putative (potential) enrichment, you must first consider what you hope it will achieve. That way, you can measure whether it has achieved the expected goals; most putative enrichment is provided with the intention of changing behaviour (see **section 8.3**) and so data can be collected to evaluate whether this was achieved and thus whether the change to the animals' environment can be considered enriching. In some situations, multiple goals may be set for an enrichment, which makes the process of demonstrating its efficacy more problematic. It also makes comparisons of enrichments more complicated (Newberry 1995).

Previously, much enrichment has developed on a 'trial and error' basis, whereby stimuli are haphazardly added to an enclosure. But without the resultant behaviour being observed, it is not clear whether these changes to the animals' environment have a positive or negative effect, or, indeed, any effect at all. Past enrichment success probably results from the vast number of potential enrichments provided, rather than from their suitability in meeting any aims set. For example, when Delfour and Beyer (2012) systematically evaluated twenty-one objects provided to bottlenose dolphins *Tursiops truncatus* as enrichment, they found that only 50 per cent of them were effective.

Box 8.1 IS TRAINING ENRICHMENT?

The use of training, especially husbandry training, is becoming more commonplace in many zoos (see **section 13.4**). Training, based on the principles of operant conditioning, is the process of bringing the expression of some of the animal's behaviours under the control of the keepers, who use conditioned cues or commands and reinforcement to elicit them. Training can lead to benefits and it has been suggested that one of these is that it is enriching (e.g. Laule and Desmond 1998). Indeed, operant conditioning was the basis of behavioural engineering, which was the precursor to enrichment as we know and practise it today (Markowitz 1982; Mellen and MacPhee 2001). But enrichment is considered by some to have a different function and impact on animals than that observed during husbandry training. This issue is complicated further, because the apparently simple statement that 'training is enriching' seems to be interpreted in a variety of ways (Melfi, 2013).

It is probably easiest, firstly, to consider what we expect enrichment to do, and then to consider whether training can achieve this. As we have explored in this chapter, enrichment is a very broad concept. Usually, before a proposed environmental change can be considered enriching, it needs to be assigned a goal (for example, that it has the effect of reducing stereotypies), and then if the goal is achieved it is considered successful and enriching.

Alternatively, if the underlying mechanisms of training and enrichment are the same, we might be able to suggest that they both have similar impacts on the animal. As yet, although there is a large body of data from enrichment studies, there is little on the impact of training. Hare and Sevenich (1999) proposed that enrichment and training could be thought of as sharing four similar mechanisms:

1. a **stimulus** that triggered the behaviour;
2. a window of opportunity during which the behaviour could be expressed;
3. the behavioural response itself;
4. the connection between the stimulus and behavioural response.

However, when they compared these mechanisms in an enriched and a trained tiger, they concluded that the four mechanisms were functionally very different (**Fig. 8.16**). This suggests that we cannot automatically consider training and enrichment to have the same impact on animals.

There are not sufficient data to support or disprove that training is enriching *per se*, but we do know that training has an important function in animal husbandry regardless and should be part of animal management programmes (Forthman-Quick 1984; Reinhardt and Roberts 1997).
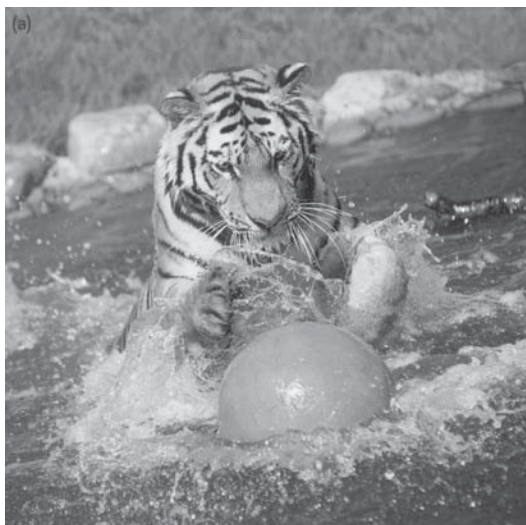
Figure 8.16 Here you can see (a) a tiger *Panthera tigris* with a traditional enrichment item at Vienna Zoo, and (b) another tiger being trained to target at the Bronx Zoo. These are both very different activities. Do you think that they are both enrichment? (Photographs: (a) Vienna Zoo; (b) Vicky Melfi)

Figure 8.17 'SPIDER' is an acronym for the stages that should be considered when implementing behavioural husbandry changes, whether they are enrichment, training, or modifications to the animals' housing and husbandry. The level of formality necessary for each stage can be tailored to the needs of the zoo (e.g. Colahan and Breder 2003).

They also noted that, because of individual differences, the same enrichments were not successful for all dolphins.

Ideally, a systematic method of evaluation is necessary. Simple guidelines to evaluate the effectiveness of enrichment were produced by Plowman (2006). A process developed at Disney's Animal Kingdom, referred to by the acronym 'SPIDER'

(**Fig. 8.17**), can also be helpful in determining the effectiveness of **behavioural husbandry** measures. We will return to the issue of monitoring enrichment in **Chapter 14** on 'Research'.

8.6 What makes enrichment effective?

There can be some problems associated with enrichment provision and it is true that they are not all as successful as each other. For example, food enrichments are consistently more effective than other types, including scent, tactile, and object enrichments (in domestic rabbits, see Harris *et al.* (2001); in domestic cattle, see Wilson *et al.* (2002) (**Fig 8.18**). This is why it is important to provide a planned enrichment programme, which can be organised using a timetable (see **Box 8.2**).

The likelihood that enrichment will be successful can be increased and the potential for problems limited, if the following are borne in mind. It is also important that provision of enrichment does not compromise the health and safety of the animals or those working with them. This means that all enrichments should be included in the routine hygiene regime, to minimize the risk of disease transmission, especially if being transferred between enclosures (animals), and checked that they are safe for use.

Figure 8.18 Food enrichment is probably the most popular type of enrichment provided and often proves to be highly effective. It can reflect seasonal changes in food availability, or simply follow festive holidays to promote visitor interest in the animals and/or associated issues, like (a) here at Paignton Zoo Environmental Park the provision of pumpkins at Halloween to porcupines *Hystrix africaeaustralis*. Alternatively, food can be used with other types of enrichment, such as (b) here at Duisburg Zoo a sensory event (a moving model zebra) precedes the provision of food to these African hunting dogs/painted dogs *Lycaon pictus* (Photographs: (a) Gillian Davis, Paignton Zoo Environmental Park; (b) Jeroen Stevens).

8.6.1 Monopolization

Providing enrichment to social groups can be extremely beneficial (Honess and Marin 2006) but, as with any resource, enrichment in a social situation can also be the cause of competition, and the extent of this depends on the natural history of the species. A joystick computer-based system was used at Zoo Atlanta as a cognitive enrichment for pair-housed orang-utans *Pongo pygmaeus*. It was highly sought after by the animals, although one member of the pair monopolized its use; high users spent 48.9 per cent of their time using the system compared with 2.9 per cent in the low users. The joystick was considered highly successful, because the level of complexity continually increased and the animals did not **habituate** to the device, as shown by the observation that use of it did not significantly decline during its presentation. Unfortunately, however, its presence was associated with increased aggression and anxiety-related behaviours (Tarou *et al.* 2004) (**Fig. 8.19**). Consequently, the authors suggested that it should only be used with singly housed animals. A later study at Zoo Atlanta found that there were no negative effects of providing a computer-controlled touch screen to a group of orang-utans (Perdue *et al.* 2012). The reason for this difference is unknown, but could result from different animals or social composition in the studies, or that the resource was perceived differently.

On the other hand, when the adult male in a group of Hamadryas baboons *Papio hamadryas hamadryas* at Johannesburg Zoo monopolized a small box filled with food, other group members simply foraged elsewhere in the enclosure (Jones and Pillay 2004). However, when a large box filled with food was provided to them, the adult male was no longer able to monopolize it and other members of the group tried to feed from it. It was only then that rates of aggression rose. When a similar protocol was applied to enrichment provision at Singapore Zoo, intergroup aggression in squirrel monkeys *Saimiri sciureus* was seen to rise and affiliation reduce when single-use enrichments were provided, compared with group-use enrichments (Sha *et al.* 2012); both forms of
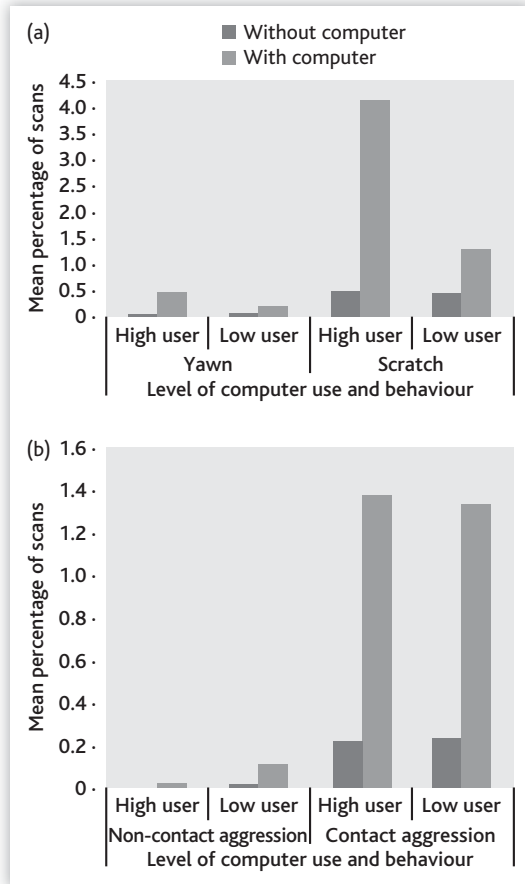
Figure 8.19 A highly complex cognitive enrichment provided to orang-utans *Pongo pygmaeus* required pairs of animals to manipulate a joystick, connected to a computer program. Unfortunately, the enrichment was so highly prized that (a) mean percentage scans of anxiety-related behaviour increased after the introduction of the enrichment, as did (b) aggression. However, it should be noted that the frequency of these behaviours was still low, even after the introduction of the enrichment. (From Tarou *et al.* 2004)

enrichment significantly reduced stereotypies. These examples demonstrate how differently social structures operate and how monopolization leads to competition in one context, but does not do so in another. It is important to consider how the social structure operates for any group that is given enrichments. As a rule of thumb, it is best to provide enough enrichment for all animals in the group—and, sometimes, for a couple more, if the animals are able to collect, hoard, or carry more than one of the objects.

Potentially, monopolization can also occur in mixed-species groups. However, provision of food-based and sensory enrichments to a mixed group of nocturnal animals (nine-banded armadillos *Dasypus novemcinctus*, Senegal bush babies *Galago senegalensis*, and two-toed sloths *Choloepus didactylus*) did not lead to conflicts between the species over enrichments (Clark and Melfi 2012).

8.6.2 Novelty versus habituation

Another matter of contention concerns for how long the enrichment is effective. Previously, the rationale of much enrichment has been based on its novelty value, and it has aimed to stimulate interest and exploratory behaviours in the target animal. The big problem with using novelty as the basis for enrichment, however, is that once it is known, it is no longer novel. It will then lose its appeal to the animal and will no longer represent enrichment.

For example, the use of a mealworm feeder by common marmosets was seen to decline steadily in a 3-hour session, despite food being continually dispensed (Vignes *et al.* 2001). Initial use of the feeder by the animals was associated with declines in pacing and sitting behaviour. The marmosets' loss of interest in the enrichment in this study follows a familiar pattern observed elsewhere when enrichments are repeatedly provided or left in an enclosure for a prolonged period—their effectiveness lessens. This may have occurred because the marmosets were now satiated, but it may also represent habituation (see **section 4.1.2**).

The speed and level of habituation seem to vary. For example, Brent and Stone (1996) observed that singly- and pair-housed laboratory chimpanzees continued to interact, even at low levels, with a variety of enrichments that had been available to them continuously for some months: television (22.75 months), a ball (55.9 months), and a mirror (25.9 months). Sumatran tigers at Paignton Zoo Environmental Park were shown to habituate more slowly to food-related than to scent enrichments (Plowman and Knowles 2003). Habituation was ameliorated if a 3- or 4-week gap was left between repeating enrichment items, and levels of pacing would remain low, indicating that the enrichments were successful (**Fig. 8.20**).

It has been suggested that habituation can be minimized if the enrichment is (i) cognitively
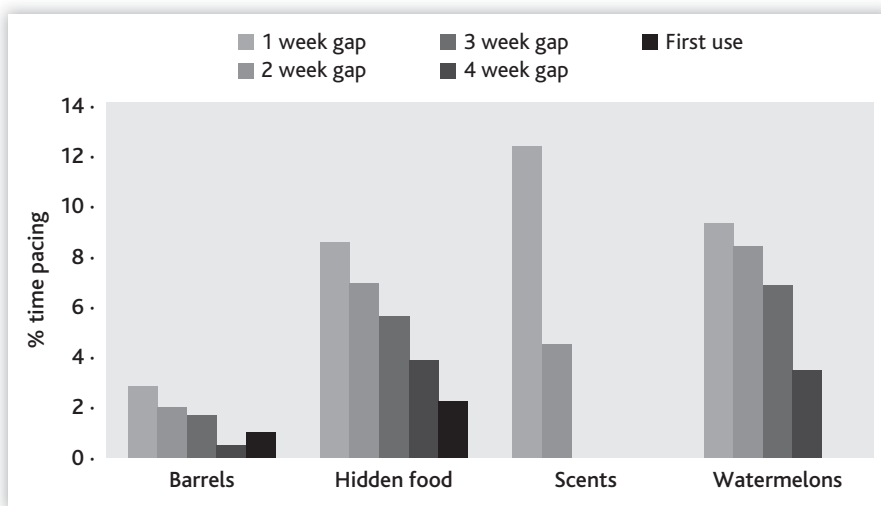
Figure 8.20 The goal of the various enrichments given to two Sumatran tigers at Paignton Zoo Environmental Park was to reduce the percentage of time they spent pacing. As such, when levels of pacing increase, it is considered that the enrichment is no longer effective and that the tigers have become habituated to it. As the gap left between repeating the enrichment (i.e. 1, 2, 3, or 4 weeks) increased, the percentage of time spent pacing reduced, illustrating that the habituation could be reduced. (From Plowman and Knowles 2003)

Box 8.2 USING ENRICHMENT TIMETABLES CAN MAKE PROVISIONING PRACTICAL

Practical enrichment provision requires a great deal of organization to ensure that all animals receive different types of enrichment and, importantly, that enrichments are removed after use (daily) to prevent habituation. Different enrichment timetables have been developed over the years, with two main aims: ease of use by keepers, and ensuring that a diverse array of species-specific enrichments are provided for the animals.

Keeper-friendly timetables have been designed, which are organized on blackboards or with fridge magnets, tick sheets, or specially designed computer software. All these timetables include features that enable all keepers to keep track of which enrichment has been used and which is due, because work schedules mean that not all keepers will work together at all times. An often quoted factor limiting provision of enrichment is a lack of time (Hoy *et al*. 2010). Formalizing an enrichment timetable can reduce the time taken to implement enrichment, as the planning has already been done.

Although it is desirable to study empirically the impact of each and every enrichment or determine when an animal has become habituated to it (no longer interested in it), in practice, this is not always possible usually because of limitations on time or expertise. Equally, it is likely that enrichment programmes will have limited impact if the same few enrichments are repeated frequently, or if the creation of new enrichments cannot be sustained in the long term. So Wojciechowski (2001) suggested that each enrichment could be used for two days, by replenishing it (with food or fresh scent etc.) or moving it on the second day. These actions were reported to sustain the animals' interest in the enrichment, above that observed if the enrichment was just left in the enclosure.

For ease of implementation, enrichments can be grouped into different categories and rotated. For example, at Paignton Zoo Environmental Park, enrichments are characterized as food-based, sensory, or manipulative (Dobbs and Fry 2008). In these timetables, primate species receive different types of enrichment, which are refreshed on the second day, ensuring that an enrichment will only be used every 2–3 months (**Fig. 8.21**).

Various other enrichment programmes have been designed and reported in *Shape of Enrichment*, the proceedings of the International Conference for Environmental Enrichment, and other journals and handbooks (e.g. Hooper and Newsome 2004; Neptune and Walz 2005).
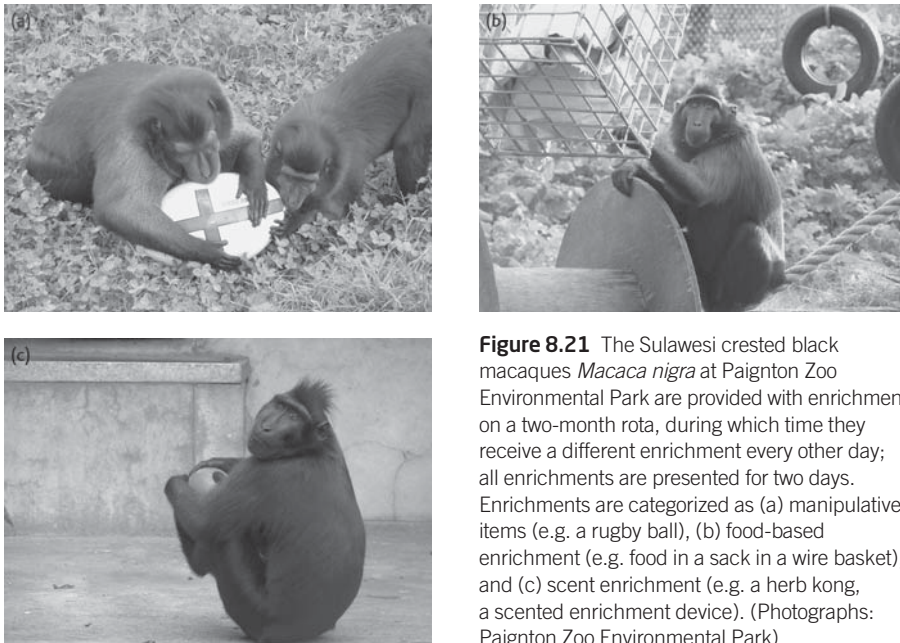
Figure 8.21 The Sulawesi crested black macaques *Macaca nigra* at Paignton Zoo Environmental Park are provided with enrichment on a two-month rota, during which time they receive a different enrichment every other day; all enrichments are presented for two days. Enrichments are categorized as (a) manipulative items (e.g. a rugby ball), (b) food-based enrichment (e.g. food in a sack in a wire basket), and (c) scent enrichment (e.g. a herb kong, a scented enrichment device). (Photographs: Paignton Zoo Environmental Park)

challenging, (ii) provides an outlet for a highly motivated behaviour, (iii) provides a contingent link between **appetitive behaviours** and **consummatory behaviours**, and/or (iv) is repeated after an interval of time.

8.6.3 Contrafreeloading: wanting to work for rewards

Animals do, indeed, appear to want to work for rewards, as originally suggested by Markowitz (1982) and as mentioned earlier in this chapter. Despite some authors considering this concept anthropomorphic, many studies have nevertheless shown that animals are willing to 'work' in order to get to a reward. More surprisingly, animals have been observed to 'work' for food even in the presence of freely available food, i.e. animals will choose to use an enrichment device (reviewed by Inglis *et al.* 1997). For example, thick-billed parrots *Rhynchopsitta pachyrhyncha*, green-winged macaws *Ara chloroptera*, and yellow-backed chattering lorys *Lotius garrulous* preferentially ate from an enrichment device, a wooden log with food hidden in it, even though food was available in a bowl (Coulton *et al.* 1997). These birds emptied the contents of the enrichment devices within 24 hours and ate from their bowls at significantly reduced rates when these devices were available.

This phenomenon has been termed 'contrafreeloading' and has been observed in a variety of captive animals, which are usually given food-based enrichment while an alternative 'free' food supply is available.

Contrafreeloading may explain why many 'cognitive' enrichments are successful. Enrichment is not usually the only source of food available, so it seems unlikely that animals use food-based enrichment because they are hungry (although the food chosen may be particularly favoured, in which case the animal may be highly motivated to get access to it). Contrafreeloading also does not necessarily provide more food. For example,

singly-caged laboratory rhesus monkeys could obtain 11.3 primate pellets in 673 seconds when using a puzzle feeder, but this was much less efficient than their 'usual' method of feeding, from which they could obtain twenty-nine primate pellets in 32 seconds (Reinhardt 1994a).

So why do captive animals choose to 'work' for food? Within **behavioural ecology**, much research has been undertaken to attempt to explain this phenomenon. Possible explanations have been presented, but most data collected support the first two of these suggested hypotheses:

- it fulfils a need to gain information about the environment—information primacy theory[4] (see Inglis and Ferguson 1986);
- it allows the animal to express species-specific behaviours—gaining food out of a bowl may not be as natural as cracking a nut (see Elson 2007);
- there is a behavioural void, because captivity does not provide enough stimulation, so animals perform elaborate behaviours when given the opportunity (Chamove 1989).

8.6.4 Providing a contingent link

The performance of species-specific goal-seeking (appetitive) and goal-oriented (consummatory) behaviours can establish and reinforce a connection that provides the animal with knowledge that is vital for survival (Misslin and Cigrang 1986). For example, an animal that is motivated to forage (appetitive) may wander through some long grass and be rewarded by finding insects, which it eats (consummatory). The relationship between the two behaviours here is a contingent one; they are causally connected.

Contingent relationships give an animal predictability about the environment and hence give it a certain amount of 'control'. Shepherdson (1994) has suggested that the loss of this contingency or 'control' in a zoo animal's life could have serious

---

[4] **Information primacy theory** suggests that animals are highly motivated to learn about their environment and that, as such, they will 'work', expend energy, and behave in such a way that they are able to gain more information about their environment (reviewed by Inglis *et al.* 1997).

consequences to its psychological well-being. Maintaining this contingent link in zoos is sometimes difficult, because animals may be motivated to move away from people and not be able to do so, or may look for food and find none. A lot of research has been undertaken which demonstrates that an animal's welfare is compromised when it lacks control over its environment (reviewed by Bassett and Buchanan-Smith 2007). For example, providing giant pandas *Ailuropoda melanoleuca* with control over determining which area of their enclosure they used was associated with fewer signs of behavioural agitation and reduced urinary cortisol (Owen *et al.* 2005). Providing choice for animals and opportunities for them to gain control over the environment are difficult to quantify, but are known to confer welfare benefits (Chamove 1989; Shepherdson 1991) (see **section 7.5.2**).

Enrichment can provide an ideal method of maintaining this contingency in captivity. For example, tigers provided with scents in their enclosure are given opportunities for behavioural expression that can be rewarding in and of itself. The tiger can choose whether to walk away from the scent, or to overmark the scent with its own, to scratch or rub the scented area, or to perform the **flehmen** response.

8.6.5 Motivating the animals

An animal's motivation to undertake any behaviour (such as interacting with an enrichment) will be affected by a great many factors (see **section 4.1.3**), including species-specific biological needs and abilities, individual differences (age, sex, past experience, health status, etc.), and temporal circumstances (season, time of day, etc.). A good enrichment will be tailored to an animal, or group of animals, by considering these factors. **Behavioural economic theory** is the study and quantification of an animal's motivation to express behaviour or gain resources, and other methods can be employed to measure an animal's motivation to perform a type of behaviour or to gain access to a resource (see **section 7.4.5**).

A classic example of seasonal variation in motivation is nest building, which is only required prior to parturition or courtship. This has been studied empirically with pre-partum farmed pigs. Gravid (pregnant) pigs show a high preference for straw pre-partum; when this is provided, it stimulates significantly more nest-building and rooting behaviour, and decreases the risk of the mother crushing the piglets (Thodberg *et al.* 1999).

8.6.6 Providing opportunities for behavioural expression

It should be clear by now that well thought out enrichment will provide opportunities for behavioural change. In this case, it is essential that we do not underestimate the potential of animals, either because of our lack of knowledge of them, or because our observations of what they do are based on situations in which their housing and husbandry are not ideal. For example, it has been theorized that **ectothermic** reptiles are unlikely to express play. Nevertheless, provision of objects such as balls, sticks, hoses, etc. to a Nile soft-shelled turtle *Trionyx triunguis* at the National Zoo in Washington, DC, led to extensive vigorous play-like behaviour and a reduction in self-injurious behaviour (Burghardt *et al.* 1996). Furthermore, prior to the provision of four enrichment items (**Fig 8.22**), three loggerhead turtles *Caretta caretta* and one blind green turtle *Chelonia mydas* spent about 77 per cent of their time resting or pattern swimming (Therrien *et al.* 2007); the latter is considered to be a stereotypical behaviour. When enrichment items were present the turtles spent 88 per cent of their time in random swimming, and a further 8 per cent in focused behaviour; both were considered to be positive changes in behaviour.

Intuitively, we may think that older animals may be more difficult to enrich; certainly, they are likely to be less agile than their younger counterparts. Swaisgood *et al.* (2001) found that adult giant pandas were less responsive to enrichments than sub-adults, although both were more receptive to food enrichments. Novak *et al.* (1993) found that age did not affect enrichment use in group-housed laboratory rhesus macaques, and older females would manipulate objects extensively. They observed that social facilitation and avoidance
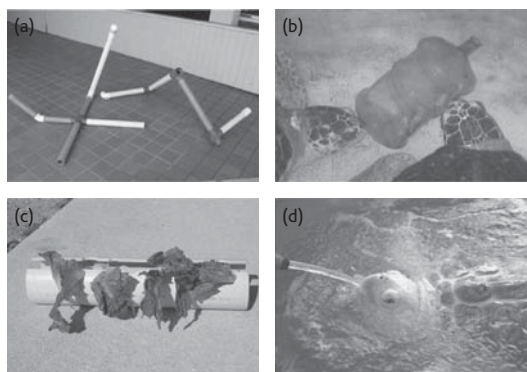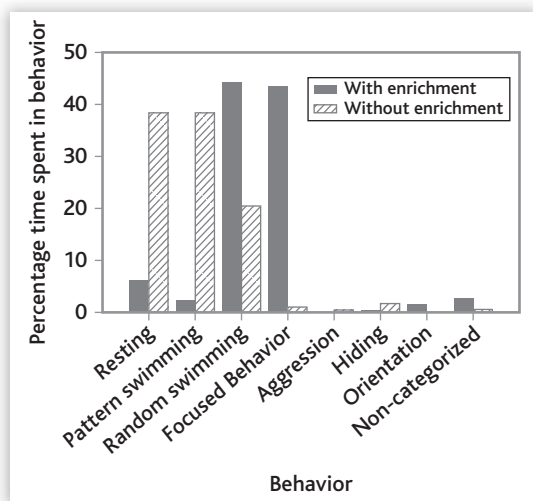
Figure 8.22 Sea turtles were provided with four different enrichments: (a) two polyvinyl chloride (PVC) tubes; (b) a food-filled plastic water cooler dispenser with holes cut into the side, so the turtles could access the food; (c) a PVC lettuce feeder; (d) a hose dispensed water into the pool. When these enrichments were provided all turtles ($N = 4$) spent significantly less time performing pattern swimming and significantly more time performing random swimming and focused behaviour. (From Therrien *et al.* 2007)

played a role in enrichment use, and suggested that this demonstrated that housing was a larger determinant of enrichment than age. But contrary evidence was provided by Brent and Stone (1996), who found no effect of housing on enrichment use in singly- and pair-housed chimpanzees.

8.6.7 People

One of the biggest hurdles to overcome in providing effective enrichment is people, or (more diplomatically) the different needs and priorities of people within an organization.

Hare *et al.* (2003) describe how a comprehensive enrichment plan was set up for giant pandas, and how this was successful mainly as a result of considering '*staff time and effort, institutional requirements, resource availability, visitors' experiences and research protocols*'.

8.7 The benefits of environmental enrichment

Full appreciation of the impact of enrichment has not yet received much attention in zoos, which see their key aims and goals to be modifying behaviours or promoting behavioural diversity (**Plate 8.1**). But research conducted on laboratory and farm animals, where a greater array of indices can be measured, has highlighted that there are many other, more far-reaching, benefits of providing enrichment.

Behavioural expression is determined by neural activity, so if enrichment can modify behaviour, it is logical to assume that the brain and associated neural networks are also affected (Carlson 2007). In fact, enrichment does have a considerable effect on the morphology, development, and function of the brain, and consequently behaviour (Van Praag *et al.* 2000), and neurogenesis can be promoted through the use of enrichment. Both old (aged 25 months) and young (aged two months) laboratory-housed Wistar mice provided with enrichment showed increases in neurogenesis in the hippocampus (Segovia *et al.* 2006). The hippocampus appears to be involved particularly with the 'encoding' of information about the environment; it is then stored, elsewhere in the brain, as long-term memories. The cerebral cortex, the area of the brain associated with 'higher' cognitive processing (for example, problem solving or complex movement), appears to be even more receptive to enrichment than other parts of the

brain (Diamond 2001). Neurotrophins, proteins associated with a variety of neural cell activities, increase within several regions of the rat's brain when the animal is provided with enrichment (Ickes *et al.* 2000). Increased levels of neurotrophins have been associated with enhanced visual cortex plasticity and the ability to change and be flexible, among other things. Prusky *et al.* (2000) noted that the enriched mice had higher visual acuity than their unenriched counterparts.

It has been known for a long time that enrichment enhances learning and memory in rodents (Hebb 1947). More recent studies have demonstrated that enrichment increases brain plasticity and this enables adaptation to environmental changes, which, in turn, influences learning and memory throughout life. For example, Sneddon *et al.* (2000) demonstrated that pigs provided with enrichment (additional space; the availability of peat and straw in a rack) learned more rapidly than those without. These learning tasks included operant conditioning tasks and navigation around a maze. Learning deficits resulting from lead exposure have also been shown to be reversible with the provision of enrichment (Guilarte *et al.* 2003).

Enrichment can also affect an animal's interactions with its environment. A number of studies have demonstrated that fearfulness can be reduced in animals that have been provided with enrichment (e.g. Reed *et al.* 1993). For example, orange-winged Amazon parrots reared in enriched enclosures have been shown to interact with novel objects more quickly with shorter latencies than conspecifics reared under 'normal' conditions (Meehan and Mench 2002). These results led the researchers to suggest that enriched conditions can successfully modify the fear responses of captive animals.

Furthermore, the physical exercise associated with enrichment has been shown to contribute to recovery from brain damage and the deleterious effects of ageing (Jones *et al.* 1998). Providing enrichment has also increased recovery post-trauma (Jadavji *et al.* 2006). Thus, animals that need surgery can also benefit from enrichment, as in the study by Coviello-McLaughlin and Starr (1997) which found that mice provided with preferred nesting materials were less likely to 'agitate' wounds.

Enrichment can also promote breeding. Egg laying in captive orange-winged Amazon parrots is more likely if they are provided with enrichment (Millam *et al.* 1995). Indeed, in a review of the impact of environmental enrichment on the reproduction of captive animals, Carlstead and Shepherdson (1994) concluded that several indirect benefits of enrichment improved reproduction. Other benefits included the modulation of stress, socio-sexual stimulation, and changes in physical and psychological fitness.

Currently most studies that have identified non-behavioural (or indirect) benefits of enrichment have been on either laboratory or domesticated species; whether similar benefits occur for zoo animals provided with enrichment is not known. However, we can hope that, as we continue to study the impact of enrichment, we will discover that its benefits go well beyond what we initially expect, or see, not only in laboratories and on farms, but in zoos as well.

Summary

- Enrichment broadly refers to any change to an animal's environment that leads to a positive outcome and thus brings about improved or enhanced welfare.

- Enrichment is thought to stimulate captive animals both mentally and physically.

- Enrichment methods are highly variable and their success cannot necessarily be generalized between species, or sometimes even between individuals.

• Any change made to an animal's environment that aims to enrich should be appropriately monitored.

• Enrichment can sometimes provide a more dynamic environment, in which animals can display more choice and control over their lives, but this can be hard to quantify, because it may not lead to obvious behavioural changes.

• There is good scientific evidence that enrichment is extremely beneficial to animals on many levels and that, if it is incorporated into a wide variety of housing and husbandry regimes, it improves animal welfare.

Questions and topics for further discussion

1. Who was instrumental in the development of the enrichment concept?
2. How do behavioural and environmental enrichment differ from each other?
3. Discuss three enrichment aims and detail their limitations.
4. Identify, giving examples in each category, the five categories into which enrichment can be classed.
5. Why is it important to evaluate the effectiveness of enrichment?
6. Discuss three methods of increasing the likelihood that enrichment will be effective.
7. What non-behavioural benefits may be associated with the use of enrichment?

Further reading

There are various sources available in which you can find out more about the background and theory of environmental enrichment, including the comprehensive book by Young, *Environmental Enrichment for Captive Animals* (2003), and Markowitz's older, but still very relevant, *Behavioral Enrichment*

in the Zoo (1982). There are also conference proceedings of the International Conferences on Environmental Enrichment (ICEE), which are available from The Shape of Enrichment Inc., and those of meetings held by the Regional Environmental Enrichment Conferences. Proceedings from the first ICEE meeting are published in the form of a book by David Shepherdson and colleagues, *Second Nature: Environmental Enrichment for Captive Animals* (Shepherdson 1998). There is also a huge wealth of information, especially on the implementation of environmental enrichment, the considerable variety of enrichments available, and the numerous species that can benefit from enrichment, in the quarterly publication *Shape of Enrichment*, which is available from the organization of the same name.

Websites and other resources

The Shape of Enrichment Inc. (**http://www.enrichment.org**) is a not-for-profit international organization that promotes, through its quarterly newsletter, training workshops, and international and regional conferences and meetings, the implementation of enrichment. A subgroup of Shape is the Regional Environmental Enrichment Committees (**http://www.reec.info**) which provide grass-roots support for the international organization.

Other useful websites are the comprehensive site hosted by Disney's Animal Kingdom (**http://www.animalenrichment.org/**) as well as practical tips from Honolulu Zoo (**http://www.honoluluzoo.org/support-the-zoo/environmental-enrichment-program.html**).

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.
http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Chapter 9
Small population management

Most captive populations in **zoos** today are largely composed of captive-bred, rather than wild-born, animals. Conway (1986b) noted that more than 90 per cent of mammals and some 75 per cent of birds in **accredited zoos** in North America had been born in captivity. The number of captive-bred animals and the ratio of captive-bred to wild-caught animals recorded in zoos worldwide increased dramatically between 1971 and 1981 (as reviewed for several species in the orders Carnivora, **Perissodactyla**, and Primates by Knowles (1985)).

This suggests that our knowledge of and ability to manage **exotic animal** reproduction in zoos and aquariums has greatly advanced in recent times. The incorporation of reproductive technologies, as summarized in **section 9.4**, highlights that advances in captive breeding are continuing. It is worth noting that considered and careful management of zoo populations requires that as many, if not more, animals should *not* breed in zoos as those that should, although many zoos refer to the activities related to the captive management of species as 'captive breeding' or captive breeding programmes. However, this label perhaps implies that all programmes are initiated and managed with the ultimate goal of increasing the population size. This is not always the case; in fact the ultimate goal is that animals in zoos will be part of self-sustaining populations, which might mean that for some populations they are managed so as to remain stable in number, whereas others might need to be reduced over time. It is probably more appropriate to refer to all these activities, including the programmes themselves, as **captive management programmes** or 'captive assurance populations'. Though there are many principles common to managing all populations, the fact that zoo populations are small exacerbates potential genetic, demographic, and behavioural difficulties faced in population management. Historically, these small populations have arisen from poor reproductive performance in some species and restricted reproduction in others, which is constrained by space limitations (see **section 10.3.2**). Data on the reproductive biology of exotic animals are sparse, because nearly all formal studies of reproductive biology have been of only fourteen domestic species, including man and domesticated animals such as the cow, mouse, chicken, and cat (Wildt *et al.* 2003). These studies provide us with a good understanding of the physiology, endocrinology, and genetic underpinnings of reproduction, but much this of information is not directly applicable to breeding wild animals in zoos. There are also considerable differences in reproductive biology between seemingly related species. This restricts our ability to generalize across **taxa** and means that many recommendations, for example protocols for **artificial insemination (AI)** (Stone 2003), must be worked out species by species.

We will start this chapter with a brief summary of the theory underpinning our knowledge of reproductive biology and then identify some of the environmental factors that can affect decisions about whether or not breeding is recommended, and associated ramifications for small population management. We will also summarize the knowledge and techniques available to zoo professionals on which decisions are made about whether animals are allowed to breed with or without intervention, and

what these interventions may be. This is followed by an overview of the management programmes that operate under the banner of the main regional zoo associations. Finally, we will discuss what is meant by the term 'self-sustaining population', and the general methods currently implemented, and those recently proposed, which aim to achieve this.

We will cover the following topics in this chapter.

As with the other chapters in this book, several related issues are considered in the boxes, which include some supporting theory and also discussion of some more contentious issues, such as whether or not to hand-rear animals and what to do with surplus animals.

9.1 Reproductive biology

Effective captive management in zoos as part of the conservation of an endangered species requires a multidisciplinary approach, combining knowledge gained from reproductive physiology, endocrinology, genetics and population biology, ecology and behaviour, veterinary medicine, and nutrition (**Fig. 9.1**). The underlying theory of some of these disciplines is summarized in other chapters, but, here, we review some of the theory that underpins

Figure 9.1 There is a tendency to think that reproductive biology all rests on one behaviour, but in fact the success of our captive management programmes, whether there are recommendations to breed (such as these two armadillos Dasypus novemcinctus) or not, is far more complicated, as we will find out in the chapter. (Photograph: Jeroen Stevens, Duisburg Zoo).

our knowledge of reproduction and forms the basis on which we make decisions about captive management in zoos. As we mentioned earlier, much of this knowledge has been gained from studies of common domestic breeds and we are now learning rapidly that diversity in reproduction biology is as great as the diversity of species we hold in zoos (Wildt *et al.* 2003). Because the process of reproduction has evolved to transfer our genetic material into the next generation, this is where we will start.

9.1.1 Genetics

Genetics is about the way in which various features of the organism's structure, physiology, and behaviour are inherited. The gene itself is a section of deoxyribonucleic acid (DNA), which carries the code for making a protein, or part of a protein (that is, a peptide). Because proteins form a large part of the structure of the body (for example, collagen which holds tissues together, and actin and myosin which form muscle), and are also actively involved in assembling and running it (for example, as enzymes and hormones), the set of genes that an individual contains—that is, its **genotype**—can be thought of as the assembly and running instructions of the final body—that is, the **phenotype**. At least one complete set of genes is found in each cell of an organism's

Figure 9.2 During the process of meiosis, the DNA molecules become shorter and fatter so that they are visible as chromosomes. The chromosomes of a pair (one originally from the mother and one from the father) separate from each other and each goes to one daughter cell, so the daughter cells have half the genetic constitution of the parent cell.

body; within each cell, this may be only one strand of DNA, but is usually several, with the precise number depending on the species. DNA strands are long and thin, but, when they divide (at the time that the cell divides), they coil up such that they become shorter and fatter, and easily visible under a microscope. At this stage, they are known as **chromosomes**.

Cell division usually occurs to produce more copies of the cell; thus, it is a part of the growth and replacement of cells and tissues. In this sort of division, known as mitosis, the DNA also replicates itself, so that each daughter cell contains the same amount of DNA as the original parent cell. In most sexually reproducing organisms (discussed in **section 9.1.2**), each cell contains two copies of each DNA strand (and hence, of course, two copies of each gene), one inherited from one parent and the other from the other parent (known as 'diploid cells'). Because of this, cell divisions to produce sex cells (for example, ova and sperm) cannot be mitotic, because this would lead to subsequent generations with four, then eight, then sixteen, and so on, copies of the genetic material. Instead,

a different sort of cell division through reduction (meiosis, as illustrated in **Fig. 9.2**) occurs,[1] in which the two copies of each DNA strand are separated from each other into different daughter cells, which thus have only one complete set of DNA instead of two (known as 'haploid cells').

During sexual reproduction, an animal inherits one copy of each DNA strand from each parent and hence two copies of each gene are present. The two copies of each gene may not be identical; if they are, the organism is said to be **homozygous** for that gene. But genes commonly occur in several varieties, known as **alleles**, and thus the organism may have two different alleles of the gene (that is, it may be **heterozygous**). In some cases, one allele may mask the effect of the other, in which case the alleles are known respectively as 'dominant' and 'recessive'. In this case, the recessive allele only shows its effects in the organism's phenotype if it is homozygous. An example is fur colour in cats and some other mammals, where an allele for one of the genes involved in the production of the pigment melanin might fail to produce

---

[1] **Mitosis** is a process of cell division in which one cell divides to become two daughter cells, the two cells divide to become four, and so on, and the genetic information in each of the cells remains identical. In **meiosis**, on the other hand, one cell divides to become two, but the genetic information contained within the daughter cells is different in each cell because of the separation of the two chromosomes of each chromosome pair.

the required enzyme, resulting in animals that, if they are homozygous for that allele, have no skin or fur pigment, and thus are albino.

The ultimate source of new alleles is gene mutation, in which the physical structure of the DNA is changed, for example through faulty copying during mitosis. New alleles may affect the organism's phenotype in a way that is advantageous or is detrimental to the organism's ability to function. Thus, they are subject to **natural selection** and, as a consequence, may increase or may disappear from the population.

Over evolutionary time, then, populations can be thought of as being made up of all of the alleles of their constituent members, referred to as the population's **gene pool**. Different populations of the same species exist that are unable to breed because of, for example, geographical barriers. Even within the same species, different populations will have slightly different gene pools, because they live in slightly different environments in which natural selection will act differentially on the alleles present. Many genes are represented in the gene pool by several alleles (that is, they are 'polymorphic'), and this contributes to the overall **genetic diversity** of the gene pool and hence of the population.

9.1.2 Reproduction or sex?

'Reproduction' and 'sex' are not the same thing. 'Reproduction' is the process of producing offspring. For most vertebrate animals, this involves sexual reproduction, which requires two animals to come together so that their 'gametes' (haploid sex cells) can merge through the process of fertilization to produce a 'zygote' (a single diploid cell). The term 'sex' is commonly used to refer to the act of mating, but, strictly speaking in biological

terms, sex is a process that forms new individuals containing genes from more than one source. The gametes of males are called 'spermatozoa' (or sperm) and are produced in the testes (the result of meiosis; the process of sperm formation is known as 'spermatogenesis'). 'Ova'[2] (the singular of ova is ovum), or eggs, are the female gametes and are produced in the ovaries (also by meiosis, in a process known as 'oogenesis').

In mammals, females do not produce ova continuously, but release eggs during oestrous[3] cycles (the process of ovulation), which occur either continuously or seasonally (see **section 9.1.4**). Birds differ from mammals in that single eggs or ova are ovulated in succession (this is known as 'serial ovulation'), forming a clutch. In males, once sexual maturity has been reached, the process of spermatogenesis is continual, either throughout the year or throughout the breeding season. Fertilization occurs internally in mammals, birds, and most reptiles, whereas fertilization occurs externally in most fish[4] and amphibians.

As mentioned earlier, gametes are produced by the process of meiosis, in which the diploid cell, with a full complement of chromosomes, divides to produce haploid gametes, each with only half the complement of chromosomes. When two haploid gametes fuse during fertilization, the resulting zygote is diploid, with a (more or less) equal contribution of genetic material from each parent (**Fig. 9.3**).

In species where DNA does not determine gender, it is possible to find animals that are hermaphrodites. These animals, which include some fish and gastropod molluscs, can be born[5] as one gender and develop into the other (a phenomenon known as 'dichogamy', producing sequential hermaphrodites), but only one set of sexual organs can function

---

[2] Scientific papers about assisted reproduction usually refer to 'oocytes' rather than 'ova': these are female gametes or ova at a particular stage of development.

[3] Oestrous is an adjective, e.g. an 'oestrous female' or the 'oestrous cycle', whereas oestrus without the second 'o' is a noun, e.g. 'oestrus occurs post-partum in this species'. The American spellings are 'estrous' and 'estrus', respectively.

[4] Some fish show internal fertilization, notably sharks and dogfish, among which males can be distinguished by their possession of paired modified fins, which are used as intromittent organs (these are often referred to as 'claspers').

[5] We know that 'born' is probably not a very good way of referring to an animal that hatches out of an egg, but we are using it in a very wide sense here to avoid the text becoming too cumbersome.
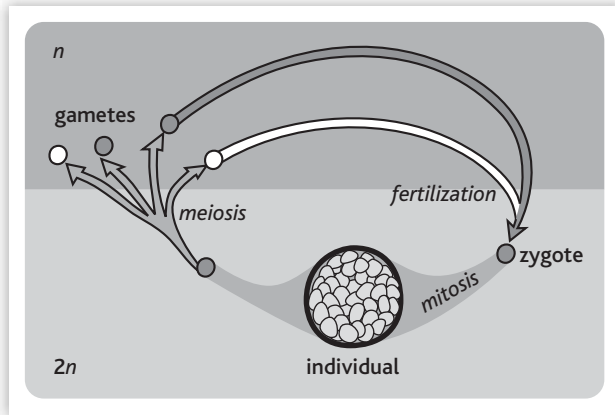
Figure 9.3 Male (sperm) and female (egg/ova) gametes are produced by meiosis, so each only has half of the chromosomes of the parent cell (referred to as haploid, or n). When they come together and fertilization results, the genetic complement of the new cell (zygote) is restored to two copies of each chromosome (referred to as diploid, or $2n$).

at one time. The process whereby an animal that starts life as a male and changes to a female later in life is referred to as 'protandry' (for example, in the clownfish *Amphiprion* spp.). The reverse, seen for example in wrasse (family Labridae), is called 'protogyny', in which an animal starts as a female, but later turns into a male. It is also possible for animals to be simultaneous hermaphrodites; examples include earthworms, some gastropod molluscs, and some fish (for example, hamlets *Hypoplectrus* spp.). Despite having both male and female sexual apparatus and thus potentially the ability to self-fertilize, this rarely happens in these species.

Alternatively, some vertebrate animals (for example, whiptail lizards *Cnemidophorus* spp.) and many invertebrates (for example, honey bees *Apis mellifera*) can reproduce asexually—that is, one parent is able to create copies of itself as offspring. Of the various processes that can underlie asexual reproduction, the most common form in animals is **parthenogenesis**. During parthenogenesis, one haploid gamete is transferred to offspring, so in animals among which XY chromosomes determine sex, the offspring tend to be female, and in those among which ZW chromosomes determine sex, the offspring are usually male (see **Box 9.1** for further explanation of this).

Parthenogenesis can be achieved via different processes. In 'thelytoky', for example, only female offspring are produced and no mating is observed (an example of this is the African Cape bee *Apis mellifera capensis*), but in 'pseudogamy' (sometimes referred to as 'gynogenesis' or

'sperm-dependent parthenogenesis'), mating is required, because the sperm 'activate the eggs' but only the maternal chromosomes are inherited by the offspring (this occurs, for example, in some salamander species). Recently, it was confirmed that the Komodo dragon *Varanus komodoensis*, thought to only reproduce sexually, was able to reproduce via parthenogenesis (Watts *et al.* 2006); this discovery was made from observation of female dragon births at Chester and London Zoos. It has been suggested that producing male offspring parthenogenetically may be a useful adaptation for an island-living female who does not have access to mates; after the production of male offspring, she would then be able to reproduce sexually (**Fig. 9.4**). Sexual and asexual reproduction have

Figure 9.4 Within the animal kingdom, reproduction can be achieved through sexual or asexual reproduction. Komodo dragons *Varanus komodoensis* have very recently been added to the list of species that can reproduce asexually. (Photograph: Vicky Melfi)

different costs and benefits, but the benefits of sexual reproduction must outweigh the costs, because sexual reproduction is widespread.

In some species, mostly invertebrates, the ability to swap between sexual and asexual reproduction has been observed (a strategy referred to as 'heterogamy'). The Komodo dragon represents one of the few advanced vertebrates in which this has been identified.

9.1.3 Endocrinology

The hormone, or endocrine, system is one of two major control systems in the body (the other is the nervous system). It releases chemical messengers, called 'hormones', which are secreted (in minute quantities) by endocrine glands and then transported in the blood to target tissues elsewhere in the body on which they exert an effect. There are three main types of hormone, classified on the basis of their chemical structure:

- steroid hormones, which include the sex hormones testosterone and the oestrogens (the US spelling is 'estrogen'), and also hormones such as **cortisol** (see **Box 7.3**), are made of rings of carbon atoms;

- protein or peptide hormones, which include oxytocin, a hormone with many effects on the processes of mating and birth;

- amine hormones, which include substances such as adrenaline (also known as epinephrine).

The action of all hormones, regardless of their chemical structure, is usually selective rather than general, because the target tissues on which they exert their effects possess receptors that recognize specific hormones.

A key part of the endocrine system controlling reproduction is the **hypothalamo-pituitary-gonadal (HPG) axis**, which is found in all vertebrates (**Fig. 9.5**). The hypothalamus is the main link between the nervous and endocrine systems in the body. It is part of the brain and secretes minute quantities of releasing hormones and other neurohormones,

including gonadotropin-releasing hormone (GnRH), which is particularly important in reproduction. GnRH, in turn, induces hormone release by the pituitary, which is an endocrine gland that sits under the hypothalamus and is connected to the hypothalamus by a structure called the 'pituitary stalk'. The pituitary consists of two sections: the neurohypophysis, or posterior pituitary, and the adenohypophysis, or anterior pituitary, which secretes a wide range of hormones including the reproductive follicle-stimulating hormone (FSH), which initiates the oestrous cycle, luteinizing hormone (LH), which, among other things, triggers ovulation, and prolactin (PRL), which is involved in lactation. These pituitary hormones are transported in the blood and, in turn, trigger a response elsewhere in the body, particularly in the gonads (testes and ovaries). As well as producing gametes or sex cells (sperm and eggs), the gonads also produce hormones. The male steroid hormones produced by the testes are known collectively as androgens, such as testosterone, while the steroid hormones produced by the ovaries are known as oestrogens, and include oestradiol and the progestins (e.g. progesterone). (Incidentally, it should be noted that steroid sex hormones are not exclusive to only one sex, so testosterone, for example, is secreted in females as well as males, albeit usually in much lower concentrations.)

In female mammals, the oestrous cycle is associated with a series of hormonal changes, starting with FSH, which initiates the cycle, and leading to the release of the ova, through the influence of LH, during ovulation. This process is illustrated in **Fig. 9.6**.

If the released ova are fertilized, further hormonal changes take place. Therefore monitoring the hormone profiles of an animal can provide an indication of whether she is cycling, anoestrus, or pregnant (see **section 9.3.4**), provided that there are enough data available describing the normal reproductive hormone profile—and, for many exotic species, these data can be limited (reviewed by Asa 1996). In humans and some non-human primates, if the released eggs are unfertilized, the endometrium (the lining of the uterus) is shed (termed
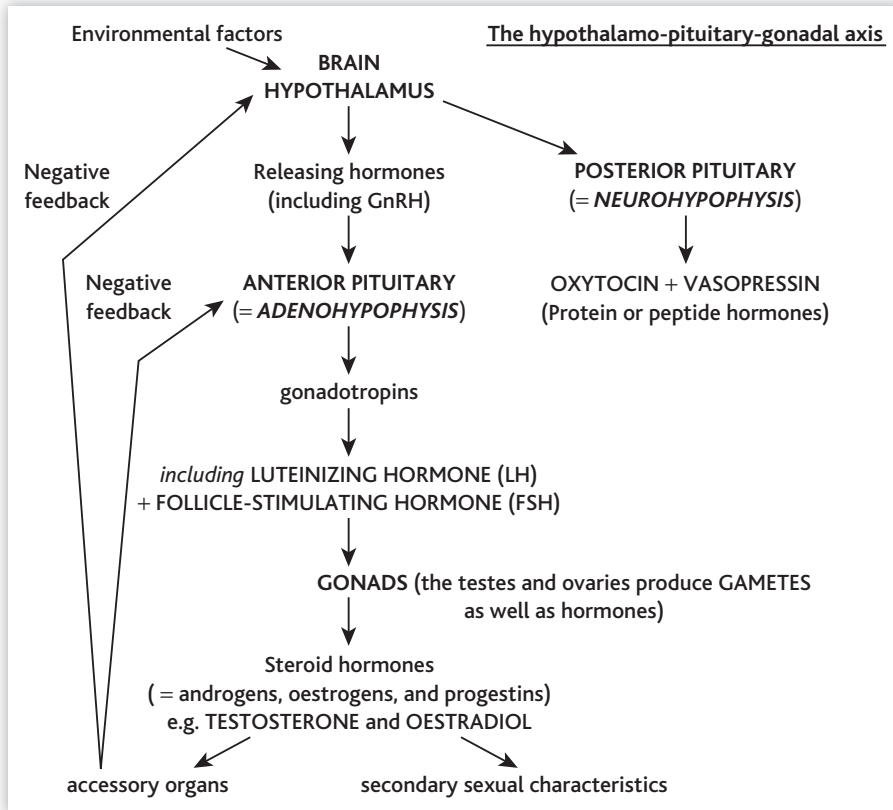
Figure 9.5 There are many endogenous and exogenous factors that influence reproduction. The hypothalamo-pituitary-gonadal (HPG) axis is central to the development and control of reproduction, which is mediated by both the endocrine and the nervous systems. The hypothalamus influences hormone production by both the anterior and posterior pituitary; these hormones go on to influence other organs in the body, including the testes and ovaries, which, in turn, are stimulated to secrete their own hormones.
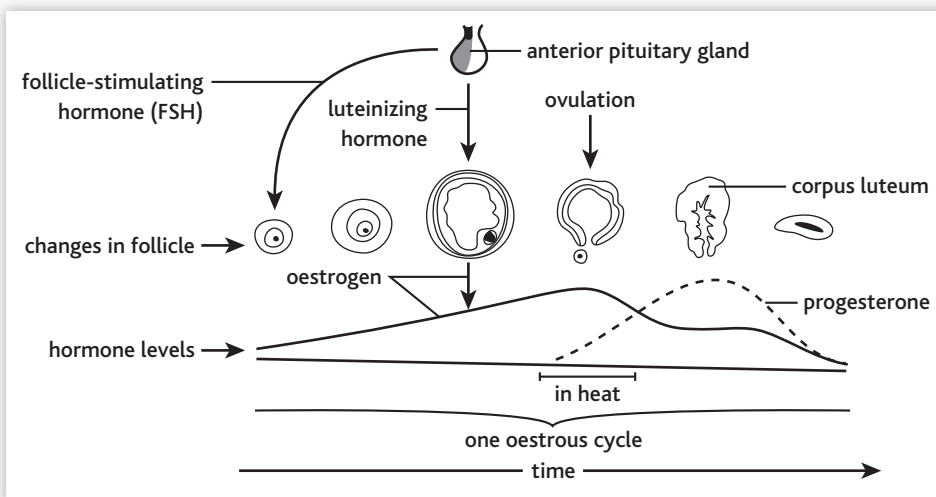
Figure 9.6 The oestrous cycle starts with the formation of a follicle, which is triggered by the secretion of follicle-stimulating hormone (FSH); as the follicle matures, it secretes oestrogen. Luteinizing hormone (LH) stimulates ovulation and the subsequent development of the corpus luteum, which produces progesterone. If the ovum is not fertilized, the corpus luteum degenerates and progesterone levels fall.

'menstruation'), so, in these species, the oestrous cycles are often referred to as 'menstrual cycles'. In other species, the endometrium is reabsorbed if the eggs are not fertilized during an oestrous cycle and thus no menstrual bleeding is observed.

Females are usually only sexually active for a short period of time during their oestrous cycles. This period of sexual activity is often referred to as an animal being 'in heat' or 'in oestrus'. It is the period during which a female is able to mate and conceive, and it is sometimes associated with changes in behaviour or external physical signs (see **section 9.3.1**). In contrast, females that have a menstrual cycle can be sexually active regardless of their position with the cycle.

Oestrous cycles start at different ages even within the same species, depending on heredity and diet. Data are mixed about whether cycling starts earlier in captive than in wild animals.

The functions of the various hormones involved in reproduction differ among taxa, even though their chemical structures may not differ much among species. For example, several progestins are found in all vertebrates, but carry out different functions. Similarly, the hormone prolactin is involved with lactation in mammals and 'crop milk' production in pigeons and doves, but is active in water retention in fish and has a non-reproductive role (in skin shedding and tail regeneration) in lizards (Nelson 2000).

9.1.4 Triggers for breeding

The time when animals are able to breed and have offspring is shaped by several factors. If breeding is synchronized with the maximum availability of environmental resources, **fecundity** (the likelihood of offspring survival) is enhanced. This synchronization can be achieved through a number of mechanisms, both internal and external, including environmental factors (such as day length and food availability), pheromones (chemical signals from other animals), and social interactions.

Pheromones are chemical signals used to communicate within a species. They are detected in a variety of ways, ranging from the receptors on the antennae of male moths, to the olfactory mucosa of mammals. Some mammals, such as felids and equids, possess a specialized organ for this—the vomeronasal organ, or Jacobson's organ (in the roof of the mouth)—and take in air carrying the pheromone molecules through the mouth, using a distinctive **flehmen** behaviour. Pheromones may also be detected from urine or other substances. These chemicals have various functions, from mate detection and selection, to hunting and territory protection, and avoidance behaviours (Wyatt 2003).

Environmental factors, including temperature, food availability, and predator pressure, help to shape the breeding biology of species. As a result, many animals have restricted periods during which they breed and have young, and these animals are termed 'seasonal breeders'. However, a few species, including some primates, pigs, mice, and rabbits, are considered 'continuous breeders', which means that they are able to breed and have offspring throughout the year. This may be because they experience sequential oestrous cycles, which makes them ready to mate and therefore have offspring throughout the year. Alternatively, it can happen in species among which mate availability is not reliable, so when a potential mate is in close proximity, this is more important in determining the timing of breeding than environmental features such as climate. These species, which include lagomorphs, felids, and camels (Lombardi 1998), have developed into **induced ovulators**, so called because the act of mating or coition stimulates ovulation and therefore makes the female ready to breed whenever an appropriate male is available.

The number of oestrous cycles and the timing of these (whether or not they are seasonal) can vary from having several cycles ('polyoestrous'; for example. felids and bovids) to having two cycles yearly ('dioestrous'; for example, canids) or only having one cycle annually ('monoestrous'; for example, some **Carnivores**). In fact, polyoestrous animals rarely experience several oestrous cycles because, if conditions are appropriate, they conceive and become pregnant, and this stops further cycles. But this system does enable females who

Box 9.1 SEX DETERMINATION AND DIFFERENCES BETWEEN MALE AND FEMALE REPRODUCTIVE MORPHOLOGY

The mechanisms of sex determination vary quite widely across different **taxonomic** groups, and whether an individual develops as a male or a female will be determined by genetic or environmental factors, depending on the species. In (nearly all) mammals, the fusion of two X chromosomes gives rise to a female (XX) and the fusion of an X and a Y chromosome gives rise to a male (XY). Ova (eggs) in mammals contribute only an X chromosome, whereas sperm may contribute an X or a Y chromosome. A variation of this system is observed in many insects; for example, in grasshoppers and cockroaches, males are determined by an absence of one chromosome (XO), although females still retain two chromosomes (XX). In birds, the situation is reversed, with males having two sex chromosomes (known as ZZ) and females having ZW sex chromosomes. Many egg-laying reptiles, including alligators, crocodiles, some turtles, and many lizards, have no obvious sex chromosomes at all. In these animals, the sex of the offspring is not determined at conception, but during a specific period of embryonic development. The factor controlling sex determination is the temperature of the nest in which the eggs are incubating. Some species (hermaphrodites) have both male and female gonads, or can function as both male and female during their life (see **section 9.1.2**).

An obvious difference between the sexes, in mammals at least, is in the visibility of the gonads or reproductive organs. While the ovaries in vertebrate animals are always internal, most mammals have testes that are external to the body cavity, contained in a pouch called the scrotum. The mammalian exceptions to this are known as the **testiconid** mammals, where the testes are internal (for example, elephants). In birds, reptiles, amphibians, and fish, the testes are always internal.

Most male mammals possess a penis, but most bird species do not and have an opening known as a 'cloaca', as do the egg-laying mammals, or 'monotremes'; exceptions include the swans, ducks, geese, and ostriches, all of which have a penis. Crocodilians and turtles also have a penis, but snakes and lizards have a pair of hemipenes—although only one hemipenis is used at any one time during copulation (**Fig. 9.7**). Tuataras (illustrated in **Fig. 9.8**), which are endemic to New Zealand and of which there are currently two extant species, *Sphenodon punctatus* and *Sphenodon guntheri*, do not actually have external sex organs, so simply press their cloacas together when mating.

Figure 9.7 The sex of all animals is not immediately obvious, because there may be a lack of secondary sexual characteristics and external sexual organs. Although invasive, one of the common methods used to determine the sex of snakes is to probe them, a technique that should only be carried out by a trained and skilled practitioner. (Photograph: Paignton Zoo Environmental Park)

Figure 9.8 Because there are various ways in which animals reproduce, the apparatus that animals use to copulate is also different. Tuataras *Sphenodon punctatus* represent a taxon in which the animals do not have external sex organs, so exchange of gametes is achieved by pressing the cloacas of both animals together. (Photograph: Geoff Hosey)
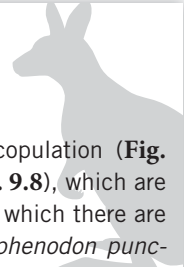
do not conceive during their first cycle to make further subsequent breeding attempts.

In seasonal breeders, of course, reproductive activity is synchronized with seasonal aspects of the environment and usually this involves day length (photoperiod). The controlling mechanism that synchronizes seasonal breeders to their environment, via photoperiod length, is mediated by the release of the hormone melatonin which is present in all animals and also in algae. In vertebrates, it is secreted from the pineal gland, a body at the base of the brain, into the blood stream during dark periods, and so the amount secreted is dependent on the proportion of dark to light in the day (Arendt and Skene 2005). It is responsible for linking many physiological and behavioural patterns into a circadian, or seasonal, rhythm (such as daily or seasonal changes in coat growth, changes in colouring and behaviour), and may also be associated with other functions, such as skin colour changes in amphibians (Filadelfi and Castrucci 1996). Long-day breeders, such as equids, come into oestrus during the longer daylight periods of spring and summer, whereas short-day breeders, which include sheep, goats, and deer (remember, we stated at the outset of this chapter that much of our knowledge in this area comes from well-known domesticated species), come into oestrus during the short daylight periods of autumn and winter. It is thought that higher melatonin levels stimulate reproduction in short-day breeders when daylight hours reduce, but repress reproduction in long-day breeders at this time. This effect diminishes when the daylight hours increase, so long-day breeders become reproductively active and short-day breeders cease to be reproductively active. However, this mechanism cannot be stimulated artificially simply by changing the hours of daylight experienced by the animals, because this process apparently involves a variety of other factors, at least in agricultural animals (Dooley and Pineda 2003).

9.1.5 Group structure and function, and mating systems

Many variables shape group size and group composition in different species, and these include habitat type, the risk of predation, and the availability of resources. Survival, over generations, is optimized when individuals adapt to the environmental conditions around them, and this can result in their developing different social organizations. For example, the formation of family units (of two breeding adults and their growing offspring) can have the advantages of allowing the members of the group to hunt together, defend a territory, and share parenting.[6]

Indeed, group size and composition, in turn, have a large impact on behaviour, affecting such things as mating strategies, feeding and foraging strategies, methods of communication, social behaviour, parenting, and social **learning**. Examples of social organizations include family units made up of parents and offspring, and single-male multi-female harems.

We have already mentioned mating systems in **section 4.1.4**, where we identified **monogamy** (male–female pair), **polygyny** (one male mating with a number of females), **polyandry** (one female mating with a number of males),[7] and **promiscuity** (breeding between multiple males and females). Examples of species that have these different mating systems are identified in **Table 9.1**.

These terms describe what these mating systems look like to us. Unfortunately, animals that live in these apparent mating systems do not necessarily behave as we might expect them to, which can make any interpretation of the advantages and disadvantages of the systems problematic, and can also lead to some confusion when housing and managing species in zoos. For example, 90 per cent of bird and 3 per cent of mammal species appear to be socially monogamous in the wild, based on the observation that they form a

---

[6] Cooperative breeding occurs if individuals other than the parents take part in parenting (Stacey and Koenig 1990; Soloman and French 2007).

[7] You might also come across the term **polygamy**, which simply means one individual mating with several others of the opposite sex, and thus includes both polygyny and polyandry.

Mating system	Number of males	Number of females	Examples	Implications for captive management
Monogamy	1	1	Gibbons, swans, beavers, the mara *Dolichotis patagonum*	High reliance on finding compatible animals
Polygamy				Need to move on offspring
Polygyny	1	>2	Lions, equids such as zebras	Potential surplus of males
Polyandry	>2	1	Marsupial mice (*Antechinus* spp.), several species of shorebirds, jacanas, pipefish	Potential surplus of females
Polygynandry	>2	>2	Red fox *Vulpes vulpes*, acorn woodpecker *Melanerpes formicivorus*, some fish species including the zebra cichlid *Pseudotropheus zebra*	Require large enclosures to reduce aggression and crowding
				Determining parentage of offspring can be difficult
Promiscuity	Any male within a group	Any female within a group	Chimpanzees *Pan* spp., cuis *Microcavia australis* (a small rodent)	Determining parentage of offspring can be difficult

Table 9.1 A summary of mating systems

bond with only one individual of the opposite sex for a prolonged period—a breeding season or, in some animals, for life. But studies of birds such as the dunnock *Prunella modularis* have shown that, if the DNA of offspring attributed to known pairings is analysed to detect paternity, males sire offspring in clutches other than their own (Davies 1992). Similar results have now been found in other bird and mammal species, and demonstrate that, rather than being monogamous, both males and females may, in fact, engage in 'sneaky matings' or extra-pair copulations; these are rarely seen and it is only recently that we have become aware of how frequent they are, because their effects can be detected in DNA analyses. Consequently, these mating systems have been referred to as 'social monogamy', but not necessarily sexual fidelity and 'genetic monogamy'. It has been suggested that as many as 90 per cent of apparently monogamous pairings actually represent 'social monogamy' (reviewed for bird species by Westneat and Stewart (2003)) (**Fig. 9.9**).

Breeding opportunities in other mating systems are also not clear-cut. In some situations, breeding can be suppressed by **conspecifics**; for example, in singular cooperative breeding species, such as common marmosets *Callithrix jacchus* and beavers *Castor fiber*, dominant females suppress conception in other females via the secretion of pheromones (Wyatt 2003). Similarly, in many social species, only the dominant male and female will breed (for example, wolves *Canis lupus*), a mechanism that is reinforced through behavioural assertions of dominance, which are associated with healthier and larger individuals (Peterson *et al.* 2002). These polygamous societies have high levels of competition between individuals, particularly between males in polygynous societies and between females in polyandrous societies. As a consequence, the more strongly competing sex may evolve marked morphological differences in size or ornaments (sexual dimorphism) or in colour (sexual dichromatism) (see **Box 9.2** for more information on sex differences). These differences

Figure 9.9 Penguins (here, a macaroni penguin *Eudyptes chrysolophus*) are one of many species that have been shown to be socially monogamous. This means that they pair for breeding, but are not necessarily faithful to that mate, and take part in extra-pair copulations. (Photograph: Living Coasts)

in morphology may make an animal more attractive to a potential mate, or more able to fight competitors, thus gaining territory and mating opportunities (**Plate 9.1**).

An alternative sexual strategy that is adopted by individuals of some species is not to appear 'dominant', but to go unnoticed, resulting in different 'forms' of the same sex. For example, orang-utan *Pongo pygmaeus* males gain breeding opportunities with females by securing territories in which females live. They secure these territories through exaggerated sexual dimorphism, becoming very large and developing secondary sexual characteristics in the form of cheek flanges. However, there are only so many territories available over which males can compete, so if a male is neither particularly big

nor very successful at competing with other large males, he may end up with no breeding opportunities. In orang-utans, then, an alternative strategy for these males is to remain small and appear 'female-like'; thus, they go unnoticed when entering the territories of other males, and may gain from 'sneaky matings' with the inhabiting females (Scharmann and van Hooff 1986).

9.1.6 Parenting

The extent to which parental care is provided, who delivers it, and for how long it is provided vary greatly among different species. Parental care is sometimes considered to lead to a bond being formed between parent and offspring, which serves to enhance the survival of the offspring (see, for example, in non-human primates, Maestripieri (2001); in **ungulates**, Lamb and Hwang (1982)). Parents also increase the likely survival of their young by virtue of their own **fitness**, which results in heritable features increasing or decreasing an offspring's chance of survival (such as 'big people produce big babies, which are more likely to survive').

The extent to which offspring are protected during their early development varies more consistently among taxa. The offspring of **viviparous** animals develop inside one of the parents (usually, but not always, the mother; male seahorses 'give birth' to live young from a pouch on their ventral surface). This strategy allows the parent to give birth to the offspring at a later stage of development when they are better able to survive. Most mammals, with the exception of the egg-laying monotremes (the duck-billed platypus *Ornithorhynchus anatinus* and echidnas *Tachyglossus* and *Zaglossus* spp.) are viviparous. This contrasts with **oviparous**, or egg-laying, animals, which need to protect their nests if they are to protect their young to the same extent as viviparous parents. Birds, without exception, are oviparous, while reptiles, amphibians, and fish show greater variability (for example, frogs and toads are oviparous, but other amphibians, such as some caecilian species, give birth to live young).
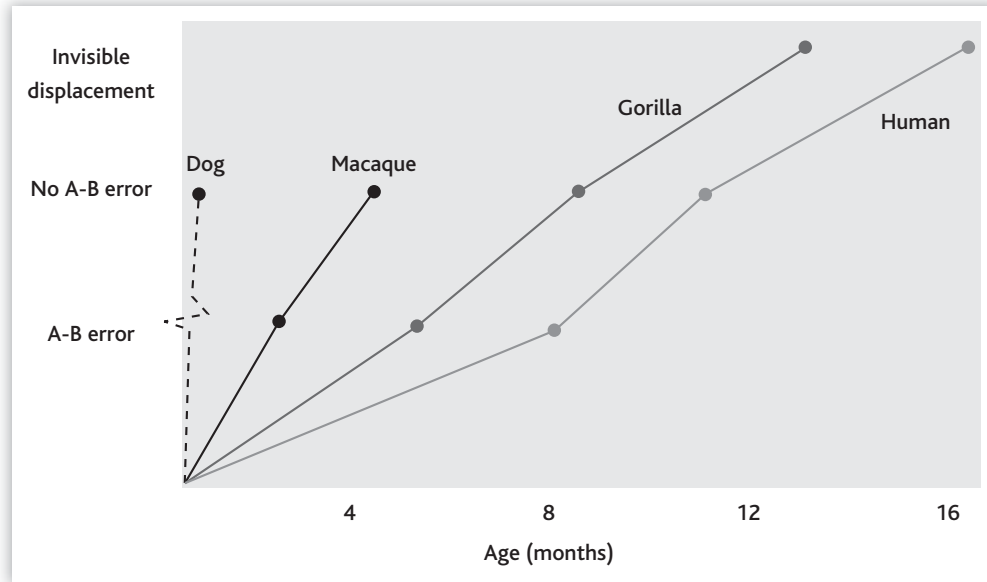
Figure 9.10 Here, we can see the speed and age at which four different species (dog, macaque, gorilla, and human) learned to find objects, and the errors that they encountered in the process. All primates were able to attain object permanence, although at different ages and different speeds, but dogs never reached this level. (From Gomez 2005)

In viviparous species, the long-term health and fitness of offspring can be affected by their parents while they are still developing inside the mother. For example, prenatal stress in pregnant laboratory rodents and primates has been identified as causing severe impairments in their offspring's development, learning, and memory (Egliston *et al.* 2007), and can have long-term effects on temperament, behaviour, and response to stress (Austin *et al.* 2005).

For those offspring that receive parental care after birth or hatching, the time at which they become independent of their parents varies considerably. For many species, the period of dependence is characterized by the young animal spending a disproportionate amount of time in play compared with adult animals: given the opportunity, juveniles have been observed to spend at least 10 per cent of their time in social play (Bekoff and Byers 1998). Both mental and physical fitness are achieved through play.

A comparative study of **cognition** has demonstrated that 'cognitive milestones' are achieved by different species at very different times. For example, object permanence—finding objects, and knowing they exist even if they cannot be seen—is considered a necessary survival skill for many species.[8] Research has shown that different species may be able to attain different levels of object permanence and at different ages; this is illustrated in **Fig. 9.10**.

9.2 Issues and constraints on reproduction in captivity

As we reviewed in the previous section, reproduction and mating strategies are very different between species and there are a great many factors that can influence whether or not breeding attempts are going to be successful. Therefore it is not surprising that breeding animals in zoos is not

---

[8] Consider, for example, a cat stalking a mouse, which runs behind a dense plant; even though it cannot see the mouse, the cat knows that it is still there, and can even anticipate where the mouse will reappear.

necessarily going to be easy and straightforward (although it can be for some species).

As we have already mentioned, fundamental information about the mechanics of reproduction, or the factors that influence it, is lacking for many of the species housed in zoos. How, then, should zoos proceed when they attempt to create and manage such a diverse collection of animals?

In the following section, we outline some of the main issues that are considered to be the basic requirements of captive management. These range from the logistical considerations of how to get the animals together, through to the genetic requirements of reducing inbreeding between individuals and maximizing genetic diversity, demographic requirements in a self-sustaining population, and, finally, to the need for behaviourally competent animals that are able to mate and rear young. As this is an applied book, we have provided sufficient coverage of these topics to give an overview and perspective of how these features can affect captive management of animals. Some other factors, such as the impact of stress, health, and nutrition on reproduction, and how captive assurance populations fit into conservation goals, will not be considered here, because they are covered more fully in **Chapter 7** on 'Animal welfare', **Chapter 10** on 'Conservation', **Chapter 11** on 'Health', and **Chapter 12** on 'Feeding and nutrition'.

9.2.1 Getting animals together for breeding

Several different approaches can be followed to bring animals together for breeding in zoos. The obvious choice is to maintain the animals in appropriate social groupings, similar to those observed in their wild conspecifics. Housing and husbandry have been, and can be further, developed to enable these types of groupings to be maintained in zoos (see **Chapter 6**).

Although natural social groups can be effective for animals that live socially and where both parents reside in the same group, many species do not live in these types of group. For example, some species are solitary, or show a fission–fusion strategy, or live in single-sex groups. Furthermore, even in stable social groups, there is natural migration of animals between groups in zoos, which is essential to prevent inbreeding between related animals. This means that, for many species, successful captive management requires intervention to overcome the complications of getting two animals together. In **sections 6.3.2** and **6.3.3**, we addressed some of these complications, including managing the tension expected when introducing animals, and managing dominance hierarchies and competition for resources. This whole process can, of course, be avoided by using artificial reproductive technologies such as artificial insemination (AI) (see **section 9.4.1**), but many zoos much prefer to bring two animals together physically to breed.

It has been suggested that there are certain housing and husbandry criteria that will ease introductions between males and females, but that an increased likelihood of successful breeding is affected by a complex set of variables. Those working in zoos will be familiar with situations in which individuals that have been appropriately matched by species, sex, age, and genetic representation do not mate when put together. This is especially a problem for the cheetah *Acinonyx jubatus* and, anecdotally, other species such as parrots. It is possible that individuals among these species express a high level of mate choice and that, if the potential mate provided does not match their requirements, they will not breed with it.

So what are these animals looking for in a prospective mate? We have already briefly considered sexual selection theory, which suggests that, in many species, individuals of the same sex compete with one another to acquire mates and, in the process, develop phenotypic differences (such as body size, weapons, ornaments, and colours) which may give them an advantage over others or signal something about their fitness. This then makes them appear more attractive

to the opposite sex and thus more likely to be selected as a mating partner (see **section 9.1.5** for more on sexual dimorphism and sexual dichromatism).

More recently, it has been found that mate choice can be influenced by the major histocompatibility complex (MHC),[9] which is an array of tightly linked genes (Boehm and Zufall 2006) found in all vertebrates except the jawless fishes (that is, lampreys and their relatives), and with a similar function in all of them. These genes are in a unique combination of alleles in each individual and enable recognition of invading molecules (such as bacteria), because these molecules have a different MHC composition. Close relatives have MHC genes that are more similar than those of non-relatives, so any animal that can detect MHC products outside the body (for example, in urine or sweat) can potentially gain information about the other animal's genetic make-up, identity, and relatedness. This detection is achieved through olfaction, often by specialized cells in the nose (Boehm and Zufall 2006) (**Fig. 9.11**). So, recognizing another individual as highly unrelated (that is, one with a very dissimilar MHC) would reduce the potential for inbreeding and thus indicate the presence of a compatible mate.

9.2.2 Genetic goals

The need to prevent inbreeding and maintain genetic diversity among our captive populations is central to how we currently manage zoo populations. Genetic variability, resulting from sexual recombination of genes, is the raw material for evolutionary adaptation. Even slight variations in genetic code can result in different phenotypes that are either more or less able to survive in a given habitat. It is this process that leads to genetic diversity in the population. In small populations, however, it is more likely that closely related animals will breed with each other and, because they

Figure 9.11 Olfaction—that is, using the sense of smell—is a prominent route for communication for many species, including many felids, and can convey a lot of information about the animal that left scent. (Photograph: Paignton Zoo Environmental Park)

have many alleles in common, they may become homozygous for recessive alleles. Recessive alleles can sometimes lead to deleterious consequences, but when heterozygous these effects are masked by dominant alleles (see **section 9.1.1**).

Unfortunately, zoo animal populations are particularly small, even when zoos combine their efforts via national and international management programmes. Most captive management programmes have an **effective population** N_E (the number of animals that actually breed and contribute offspring to the population) of fewer than a hundred animals. (See **Box 9.2** for more information on the genetic terms used in captive management programmes.) This makes these populations susceptible to problems arising from inbreeding and increases the likelihood that genetic diversity will become reduced.

It is thought that reductions in genetic diversity will impede the long-term conservation goals of captive-bred populations by potentially reducing the likelihood that these populations will be able to adapt to different wild habitats, and thus survive, when and if they are reintroduced in the future. In contrast the deleterious impacts of

---

[9] The major histocompatibility complex (MHC) is an array of linked genes found in most vertebrates. The

MHC plays an important role in the immune system, but also in other areas such as mate selection.

inbreeding depression are already visible in some captive populations and include:

(1) reduced **fertility**, seen as genetic disorders, smaller litter sizes, and reduced sperm viability;

(2) reduced reproductive output, through lower **birth rates** and increased infant **mortality**;

(3) reduced fitness, due to slower development, smaller adult size, and reduced immune function.

Current thinking among geneticists and reproductive biologists working with zoo management programmes is that 'the great majority of populations forced to inbreed will suffer deleterious and insidious genetic-demographic consequences and increased extinction risk' (Taylor 2003). Numerous examples from captive populations of wild animals support this assertion. Examples include:

- decreases in semen volume and sperm motility, both within and across species of inbred gazelles *Gazella dorcas*, *Gazella dama*, and *Gazella cuvieri* (Gomendio *et al.* 2000);

- reproductive problems and reduced survival of juvenile South China tigers *Panthera tigris amoyensis*, among which inbreeding is increasing in the small captive population, and unfortunately no wild animals exist to bolster the gene pool (Xu *et al.* 2007).

Inbreeding can also occur naturally in wild populations, especially in island-living species, where breeding opportunities are limited within the one population, and those animals that survive become more and more specialized to the island habitat (Leck 1980). The mechanisms which drive changes in population genetics are summarized in **Box 9.2**.

The importance placed upon the need to guard against a loss in genetic diversity and prevent inbreeding has led to management of most small zoo populations to be driven from a theoretical genetic perspective. A widely accepted target for captive small populations is to maintain 90 per cent (or, for larger populations, 95 per cent) of genetic diversity in a **demographically** stable population over 200 years (Soulé *et al.* 1986). There are many different factors that affect our ability to achieve these targets, not least differences in the **life history traits** of different species and animal management logistics (that is, those tasks required to move and pair certain animals). Because of this, a rule of thumb is used that requires newly paired animals to be matched according to their **mean kinship** and allowed to breed if their potential offspring would have a low inbreeding coefficient (see **Box 9.3**).

9.2.3 Demographic requirements

Monitoring and managing the demography, the shape of a population, is crucial in small population management. Demographic measures include the growth rate of a population (lamda (Λ)), birth/death rates (Mx and Qx), survivorship (Px), life expectancy (Ex), and sex–age distribution. Frankham *et al.* (2002) suggested that 'demographic stochasticity substantially increases extinction risk in very small populations, but its impact declines once populations are above 50–100 individuals … a wide range of other evidence indicates that demographic stochasticity has minor impact in populations of over 100' (see **Box 9.4**). Unsurprisingly, small populations also grow much more slowly than larger populations (Scott Mills 2006). Many zoo populations are small, so aside from managing the genetic integrity of the population, it is also necessary to consider the shape of the population.

Some of the challenges faced by small zoo population management, come from skewed sex–age distributions, namely populations with too few births and too few deaths, or where sex distribution is uneven, or does not match the housing requirements. A pyramidal sex–age distribution is desirable for most populations, whereby there are more young individuals in the population compared with older individuals. This may not occur when there are problems breeding, or where survivorship is prolonged. Furthermore, sex-biased

Box 9.2 GENETIC CHANGE IN SMALL POPULATIONS

In recent years, there have been great advances in our understanding and applications in the field of **population genetics** as the study of '*allele frequency distribution and change under the influence of the four evolutionary forces: natural selection, genetic drift, mutation and gene flow*' (Frankham *et al*. 2002).

Natural selection is the process, observed in wild animal populations, whereby the alleles of some 'fitter' animals are transferred into the next generation, whereas the alleles of 'less fit' animals are not. Fitter animals are considered to possess a greater variety of traits, and thus are more likely to adapt to different circumstances and be more able to survive, breed, and rear young more successfully than other animals; hence this process is sometimes referred to as 'survival of the fittest'. Natural selection will be greatly affected by the environmental factors at the time, which may result in different allele combinations being 'fit' at one time, but not at another.

Genetic (allelic) drift is the change in allele frequency observed in a population of animals from one generation to the next that cannot be explained by environmental factors and, as such, is considered to occur randomly. Of relevance to the captive population, genetic drift can occur when a few animals from one population become **founders** of a new population, also termed the 'founder effect'. In this circumstance, founder allele frequencies will be abundant in the new population. Equally, 'genetic bottlenecks' can occur when a large population dramatically reduces in size. If the reduction is due to random events, it is possible that the resulting allele frequency of the smaller population that is left may be very different from the larger population. This type of genetic drift can have deleterious implications for the future survival of the species, because it leads to reduction in genetic diversity and thus ability to adapt to changes in environmental conditions is greatly limited. A classic example of a species that has been affected by a genetic bottleneck is the cheetah *Acinonyx jubatus*, whose vulnerability both in the wild and in captivity has been attributed to this (O'Brien *et al*. 1985).

Mutations, as their name would suggest, are changes in the animal's genetic information, but which can have adaptive, nonadaptive, or neutral consequences for survival, thus contributing to either natural selection or genetic drift. Mutations can occur for a variety of reasons, including errors made when the genetic material is copied within the cell, through exposure to ultraviolet (UV) light or radiation, or infection from viruses. In small populations the consquences of mutations can have greater impact compared with when they arise in larger populations.

Gene flow, the final evolutionary process impacting on the genetic fitness of the popultion, is the term given to the process whereby allele frequency is affected as a consequence of animals migrating into or out of a population. However, zoo populations are closed systems, and as such gene flow is restricted. In captive animal population, gene flow can be stimulated through the creation and management of metapopulations (Lacy 2013) (**Fig. 9.23**).

From this brief overview, it is easy to see that these four forces that affect population genetics are not mutually exclusive and that the consequences of them acting together will determine the genetic make-up of a population.

populations can also occur. Sex-ratio biases in populations can occur either because there is an uneven sex ratio of offspring born or because during their lifetime survivorship is supported in one sex more than the other. Birth sex-ratio biases have been observed in different zoo populations (Faust and Thompson 2000). For some species there are adaptive advantages to producing either male or female offspring, depending on their life history, rank, or availability of resources; for example, females in good condition will have male offspring (Trivers and Willard 1973). However,

Box 9.3 PRACTICAL STUDBOOK MANAGEMENT

As we have read, there are logistic, genetic, demographic, and behavioural considerations, which should underpin small population management in zoos. However, it is more likely that decisions about population management are determined first by genetic goals, and then by demographic desires, logistic possiblities, and finally behavioural needs.

So how are zoo animal populations managed genetically? Regardless of social system, our understanding of, and therefore decisions about small population management, are based on one male and one female breeding[10]. As a rule of thumb when creating potential pairs for breeding, it is necessary to balance the need to match individuals of a similar mean kinship (MK), while ensuring that their potential offspring will have a low inbreeding coefficient (r). Various computer software packages are available (e.g. SPARKS, PMx, described in **section 5.7.3**) which can help with the calculation of these genetic measures.

The MK value calculated describes the degree to which an individual is related to others in the population, so an animal with a low MK (zero or close to it) represents an individual whose alleles are not present in other individuals in the population and is not related to other animals in the population; an animal with a high MK is related to many more animals in the population.

An animal's inbreeding coefficient (r), also known as the 'degree of relatedness', is calculated as the proportion of alleles that are likely to be shared between individuals. For example, an inbreeding coefficient of 0.5 signifies that half the alleles would be shared and is thus the calculated value for the parent–offspring relationship; an inbreeding coefficient of 0.25 indicates that a quarter of the alleles are shared and is the calculated value for the grandparent–grandchild relationship.

Ensuring that the MK values match, but inbreeding is prevented, is more difficult than it sounds, because animals that are closely related are also going to have similar mean kinships, but will therefore have potential offspring with high inbreeding coefficients.

Once the genetic conundrum is solved, it is necessary to consider the sex–age distribution of the population (demographic desires) and the logistics of getting appropriate animals together to breed, because they may not be in the same social group, zoo, or country. Finally, it is necessary for the animals to have behavioural competence (see **section 9.2.4**).

---

for some taxa, such as gibbons which are monogamous sexually monomorphic species, there are no obvious reasons to suspect that a selective advantage would be conferred by biasing the sex of offspring and, as such, it is expected that births would follow Fisher's principle, where there is a 50 per cent chance of male or female offspring (Fisher 1930; Melfi 2012b). The tendency of a bias in these latter species is suspected to be due to negative consequences of a small population—demographic stochasticity. As populations get smaller, the probability that all offspring in a given generation will be of the same sex increases, which can obviously incapacitate the long-term sustainability of a captive population.

There are some circumstances, where ironically it might be desirable to have skewed sex–age distributions. For example, when animals are maintained in harem systems there is usually one adult male housed with multiple adult females; in these instances a balanced distribution of males and females would in fact represent a surplus of males.

---

[10] Managing colony breeders or groups where maternal or paternal identification cannot be assured poses many challenges, not least because software designed to aid small population management calculates genetic coefficients based on paired breeding (see **section 5.7.3**).

Box 9.4 HOW MANY ANIMALS IS ENOUGH?

Conservation biologists involved in decisions about the management of populations of animals (whether in zoos or in the wild) need to be able to work out the minimum viable population (MVP) size (Shaffer 1981; Soulé *et al.* 1986). In very simple terms, this is the smallest population of a species that is likely to be able to avoid going extinct as a result of natural disasters or other factors. Commonly quoted values for MVP size are the population size that will ensure a 90 per cent, or 95 or 99 per cent, probability of survival for between 100 and 200 years. Of course, the MVP will vary widely between species and taxa, depending on the demographic and environmental stochasticity and other factors such as genetic variability.

Values for MVP size are calculated using computer simulations or models of the probability of extinction, given a particular set of parameters; this kind of analysis is known as population viability analysis (PVA)—essentially, PVA is a risk assessment for species extinction. PVA can be used to compare different options for the management of a population, whether in captivity or in the wild; for example, if inbreeding is shown to be a key factor influencing survival probability for a proposed reintroduction project, then greater efforts need to be made to ensure genetic diversity in the animals prior to release.

A widely used software program for running PVA and calculating MVP size is VORTEX; this package is used by the Conservation Breeding Specialist Group (CBSG) of the IUCN. Other similar computer software programs exist.

An example of how MVP can be calculated using VORTEX is provided in a study by Moehrenschlager *et al.* (2006), from the Centre for Conservation Research at Calgary Zoo in Alberta. This looked at habitat suitability and PVA for reintroduced swift foxes *Vulpes velox* in Canada and Montana. Based on the best biological evidence available, the VORTEX input values included a range of parameters and assumptions, such as the maximum age of reproduction (nine years old for females, 13 years for males); maximum litter size (eight), and an assumption of no inbreeding depression in the population. Using a baseline scenario, with no major environmental catastrophes and with an initial population of just over 1,000 foxes, the probability of extinction was zero across 100 years. The authors then modelled a number of possible catastrophes, such as a canine distemper outbreak, and found that a population of this size would be likely to survive one such catastrophic event, but not cumulative catastrophes. When severe drought and an outbreak of canine distemper were combined, the extinction probability rose to more than 40 per cent.

9.2.4 Behavioural competence

Making captive management recommendations on genetic and demographic needs alone ignores the influence and impact of the animals' daily lives, i.e. their behaviour and opportunities to breed. **Behavioural competence** is a term that has been used to describe the ability of an animal to express appropriate behaviour in a given situation. For example, we might expect a behaviourally competent animal to express courtship behaviours in response to appropriate **stimuli**, such as being paired or viewing courtship behaviour in a mate (**Fig. 9.12**). Similarly, we might expect that, after parturition or hatching, animals would perform the necessary parental behaviours, if this is appropriate for these species.

Frankham *et al.* (1986) suggested that losses in behavioural competence in captive animals were as likely to occur as genetic changes. Therefore it is important to recognize the need to preserve behavioural competence as part of the long-term conservation strategy of a species, because it is as important as maintaining their genetic integrity. One way of achieving this goal is through the implementation of suitable housing and husbandry

Figure 9.12 Even for animals that are compatible and attempt mating, the physical act of positioning often requires some practice. For example, it is easy to appreciate that a male black rhinoceros *Diceros bicornis* may need some skills to manoeuvre himself physically into the right position. (Photograph: Paignton Zoo Environmental Park)

and environmental enrichment (Shepherdson 1994) (see **Chapters 7** and **8**).

However, a note of caution is necessary at this point: just because an animal does not mate or show parenting behaviours, it does not necessarily indicate behavioural incompetence. There may be extremely good reasons why an animal does not express certain behaviours, despite the fact that all the stimuli appear appropriate. An animal that does not display appropriate breeding behaviour may not like the mate that has been selected for it, and may simply be exerting mate choice (as discussed previously). Anecdotally, it also appears that sometimes a lack of parental behaviour in an animal might reflect a problem with the offspring (for example, it may be unwell or deformed; essentially, it is not a fit and healthy animal) and so there is no biological advantage to the parent in looking after it.

9.3 Monitoring the reproductive status of animals in captivity

It is important to monitor the reproductive status of animals in captivity for a variety of reasons, not least to prevent surprise babies that are not planned and which contravene captive management recommendations, or for which preparations have not been made. It is also important to monitor reproductive status, because this information informs decisions about the following.

- When to bring animals together for mating—timing this correctly is essential to increase the likelihood that animals brought together will mate, and also to reduce the time during which potentially aggressive animals are in proximity to each other (the opposite sexes of many species do not readily coexist together).

- When to make the necessary changes to animals' housing and husbandry—increasing food rations for pregnant and lactating females (see **Chapter 12**) or the provision of nesting materials pre-partum or pre-lay.

- Interpreting observations and records made about the animals—for example, their food intake, faecal consistency, behaviour. It is obviously important that changes due to reproductive status can be distinguished from those that represent a change in health and/or welfare.

- Implementing breeding recommendations, which may require that a zoo attempts to breed (or not to breed) from particular individual animals.

The first reproductive state that should be recognized is sexual maturity, but there are many other stages of reproduction that can be monitored. Reproductive states can be determined in three ways: by observing external visible signs (such as secondary sexual characteristics); from information gained via non-invasive procedures (such as the analysis of faecal samples); and from

invasive procedures (for example, the evaluation of hormone profiles from blood). These three methods are used to varying degrees with different species, because our ability to identify reproductive states across taxa varies considerably. For example, for many mammals, external visible signs can be used to determine sexual maturity, oestrus, conception, and also when a female is ready to give birth.

Analyses of data from a large population and **epidemiological** studies can provide good estimations for the likely timing and durations of reproductive states, including the onset of sexual maturity, gestation or hatching length (thus expected birth/hatching dates), inter-birth intervals, and litter/clutch size. (The use of records is explored in more detail in **Chapter 5**.)

9.3.1 External signs

Monitoring external signs is a low-tech, low-cost, and non-invasive method of determining reproductive status, and is achieved by observing the animals daily and keeping good records of what is seen. Secondary sexual characteristics are the most obvious visible sign to look for and to monitor, and these can be highly visible in some species, as illustrated in **Fig. 9.13**. The development of secondary sexual characteristics indicates the onset of sexual maturity, while changes in these characteristics over a period of time can indicate when animals are ready to mate (**Fig. 9.14**).

Equally, in many species, weight gain in wild living males, or those in captivity given adequate access to increased food rations, signifies that they are ready to breed. A well-documented example of this is termed the 'fattening phenomenon', which is observed in male squirrel monkeys *Saimiri* sp. Seasonally, male weights may increase by more than 20 per cent of their pre-breeding season body weight (Boinski 1987). It has been suggested that this weight gain prepares males for a period of fasting that may occur while they are making breeding attempts. Seasonal changes in hormone levels (testosterone and cortisol) have also been recorded to occur during the breeding periods (Schiml *et al.* 1996).

The most notable secondary sexual characteristics in females are seen in mammals, which have mammary glands. Some female mammals also have perineal sexual swellings, which become swollen (termed 'tumescent') when the animal ovulates, providing an obvious indicator of their reproductive status (**Fig. 9.13a**). Thus, when sexual swellings are swollen, the females are ready to mate, while the cessation of cyclical swelling indicates that they have probably conceived and become pregnant. Other signs of reproductive status in mammals can include changes in vulva appearance, vaginal bleeding, and swollen mammary glands and/or nipples. In some cases, these visual displays have been shown to coincide with the sequential change in hormones observed during oestrus. In Malayan tapirs *Tapirus indicus*, for example, a swollen vulva gives a good indication of lowered progesterone levels, which indicate that the females are ready to breed (Kusuda *et al.* 2007).

A variety of behavioural changes also occur during different reproductive states. Obvious behavioural changes related to reproduction include the expression of courtship displays (**Fig. 9.15**), increased aggression and competition for resources, changes in appetite, and mating and mating-related behaviour.

9.3.2 Invasive versus non-invasive monitoring methods

For many species, visible signs of external changes associated with reproductive status are either missing or are not considered reliable enough to inform decisions about their management. This should not be surprising, given that simply sexing many species (for example, many reptiles, amphibians, and fish) can itself be problematic. So, when managing these species, information about reproductive states can be gained by direct assessment of hormone profiles, gonad status, or 'putting animals together and observing what happens'.
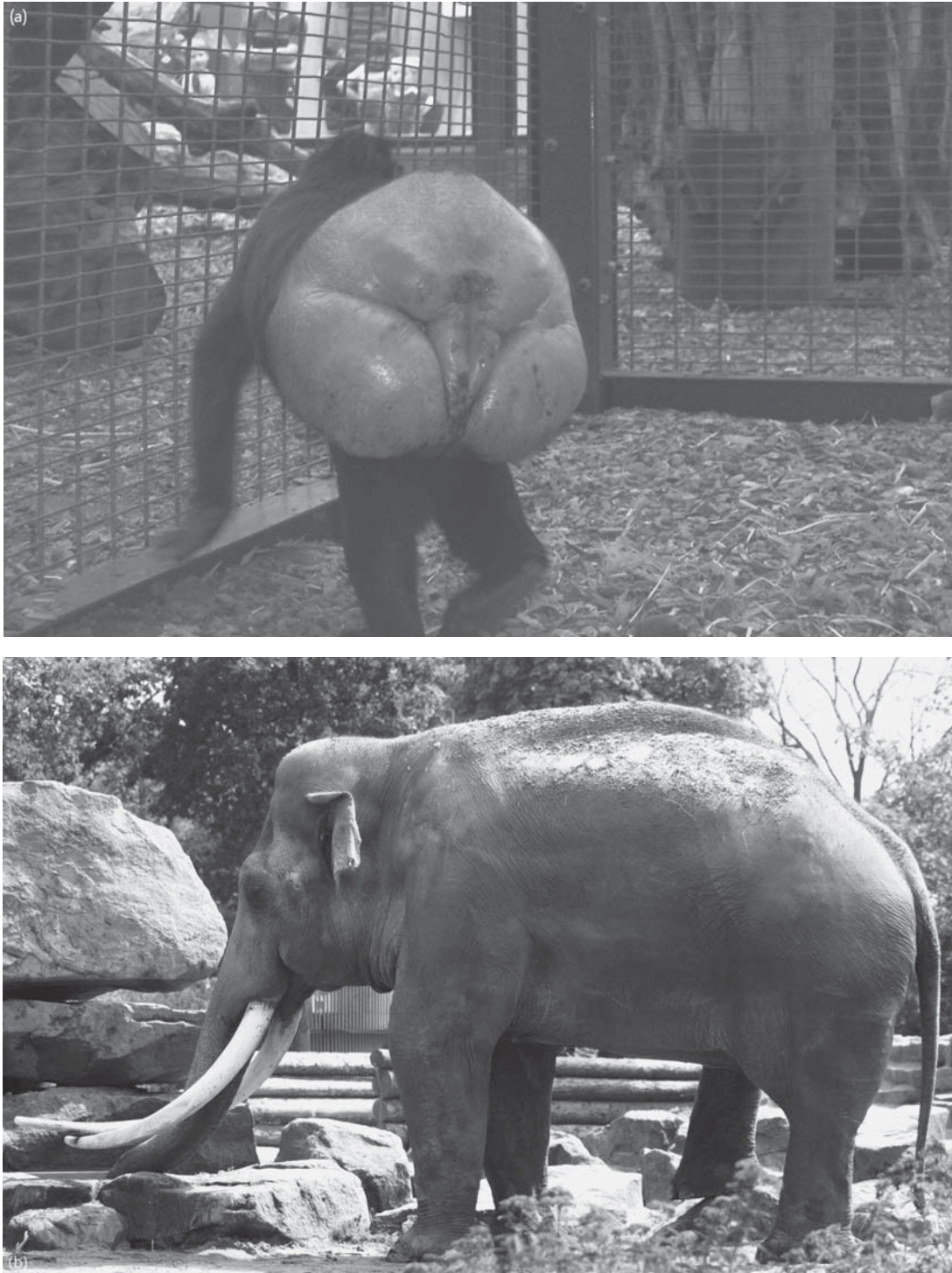
Figure 9.13 Secondary sexual characteristics are features that are unique to one of the sexes (and therefore can help us in sex determination), but which can serve to advertise information to the opposite sex—for example, (a) the reproductive status of the female Sulawesi macaque *Macaca nigra* here is advertised by her exaggerated sexual swelling—or to the same sex—for example, (b) the long tusks on this bull Asian elephant *Elephas maximus* serve as an advertisement of his fitness and deter competition from less-fit males. (Photographs: (a) Vicky Melfi; (b) Sheila Pankhurst)

Figure 9.14 It is helpful when reproductive states have external visual cues, like this chameleon *Chamaeleo calyptratus* with her distended stomach, although some visual cues can be so variable or cryptic that they are not always reliable. (Photograph: Mathias Mende)

Figure 9.15 Sometimes a change in reproductive status is accompanied by obvious behavioural changes, such as the onset of courtship behaviour, as seen in these red-tailed black cockatoos *Calyptorhynchus banksii* (Photograph: Katherina Hermann, Taronga Zoo)

There are many advantages to choosing non-invasive methods over their invasive alternatives, primarily because these methods are less disruptive to the animal. In this context, invasive refers to measures that break the skin or penetrate a body cavity, and also those that cause a disturbance to the animal. At worst, invasive methods may require that an animal is caught up and sedated, then a procedure is undertaken to monitor its condition (which may be painful), after which

it is reintroduced back into its group. Invasive procedures that may be undertaken to investigate the reproductive status of animals include taking blood samples, sperm collection, and exploratory surgery.

The impact of invasive procedures can be greatly reduced through husbandry training techniques (see **section 13.4**) or, in the case of potentially painful procedures, **analgesic drugs** can be given. Husbandry training for invasive

procedures entails the animal being trained to approach keepers and/or vet staff. Zoo staff are then able to conduct the necessary procedure while the animal remains in its enclosure and, potentially, in its social group, with minimal disruption. For example, animals can be trained to offer up an arm for a blood draw, or the anogenital region for swabs. Using husbandry training enables comprehensive and reliable monitoring, with less disruption to the animal.

Alternatively, the animal's reproductive status can be monitored using non-invasive methods. These procedures can include the use of external visible signs, as described in **section 9.3.1** (reviewed by Asa 1996), the monitoring of reproductive hormones via analyses of faeces and urine, and, in some contexts, **ultrasonography** (see **9.3.3**). Implementation of the latter can be achieved either invasively, if the apparatus must be inserted into the animal's body cavity, or non-invasively, if the apparatus can be moved over the animal's skin.

9.3.3 Ultrasonography

Ultrasonography works by using a probe that emits high-frequency sound waves. As the probe is moved over the relevant area, the sound waves are reflected from the surfaces of organs and other structures, and the reflected sound waves are received and transformed into an image (**Fig. 9.16**). For some animals (for example, dolphins) this probe can be moved externally over the skin of the animal, but, in some circumstances, greater conductivity may require that hair is clipped or a gel applied to the
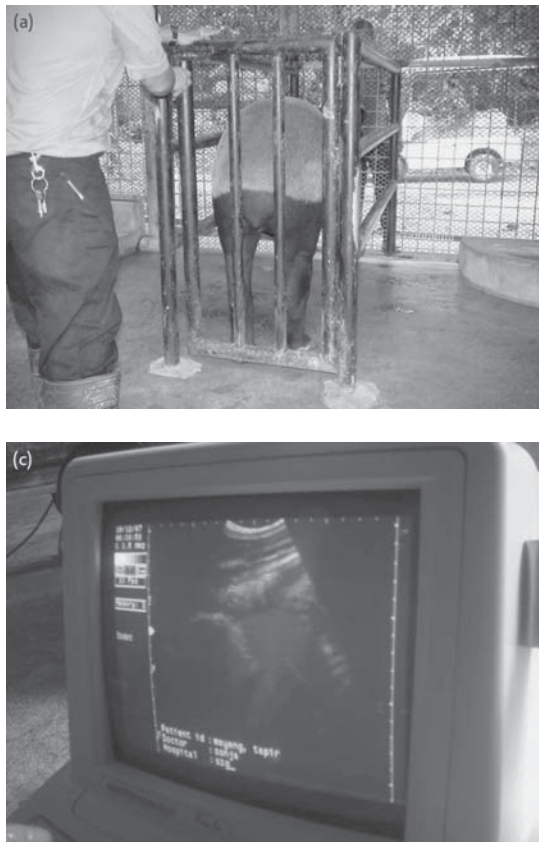
Figure 9.16 To ensure the safety of zoo staff at Singapore Zoo, this female Malaysian tapir *Tapirus indicus* is (a) crated before she is examined and (b) an ultrasound scan taken, which provides (c) images of a growing baby, enabling zoo staff to monitor the progress of her pregnancy. (Photographs: Singapore Zoo)

skin. For other species, a probe may need to be inserted into the animal, via the vagina (transvaginal) or anus (transrectal). Animals can be trained to stand while this procedure is undertaken (for example, elephants and rhinoceroses) (see Hildebrandt *et al.* 2006). Other species require anaesthesia (the big cats) or restraint (birds) before this technique can be used.

The resulting images can be recorded as: two-dimensional (2D), showing the length and width of the object of interest; three-dimensional (3D), showing length, width, and depth of the object; and four dimensional (4D), showing length, width, and depth in multiple images over a period of time, which essentially provides a video of the object and thus enables the observer to watch any movement.

Pictures captured using ultrasonography in zoo-housed animals facilitate breeding and the investigation of breeding problems; four areas where ultrasonography techniques have been beneficial are sexing animals (for example, penguins, among which the male and female may appear identical), monitoring gestation, supporting assisted reproductive technologies, such as artificial insemination (see **section 9.4**), and investigating disease.

9.3.4 Monitoring reproductive hormones

The importance of hormones in reproduction has been described already in **Box 9.1** and **section 9.1.3**. Historically, endocrine (hormone) function could only be detected and monitored using blood samples gained through invasive catch-ups of the animals, although, as we have seen in **section 9.3.2**, husbandry training can reduce the stress associated with these procedures. However, methods of non-invasive monitoring of reproductive hormones are not new (human pregnancy tests using urine samples date back to the 1920s (Cowie 1948)), although their application to the management of wild animals in captivity is relatively recent, dating from the late 1980s onwards (Pickard 2003).

Today, steroid hormone metabolite concentrations can be measured from urine, faeces, saliva, and sweat by either radio-immunoassay (RIA) or enzyme-linked immunoassay (ELISA) (reviewed for mammal species by Asa 1996). The non-invasive monitoring of hormones using assays is described in **Box 7.3**, using cortisol as the example; the principles involved are the same when monitoring sex-steroid hormones.

Research on the non-invasive monitoring of reproductive hormones in exotic wild animals has not only facilitated good animal management, but has also led to a number of useful insights into problems affecting the captive management of some species. In captive elephants, for example, ovarian inactivity affects 15 per cent of Asian elephants and 25 per cent of (female) African elephants (Brown 2000).

9.4 Providing a helping hand: assisted reproductive technologies

The three main assisted reproductive technologies (ARTs) used by zoos are artificial insemination (AI), *in vitro* **fertilization (IVF)**, and **embryo transfer** (for a summary, see Loskutoff 2003). The use of ARTs often involves surrogacy, which can take several different forms. For example, in interspecies embryo transfer, a fertilized embryo from a wild animal species is transferred into the uterus of a similar domestic species for gestation.

Zoos also make use of other reproductive techniques, such as cross-fostering (see **section 9.5.3**). Nuclear transfer (sometimes referred to as 'cloning') is now widely used for reproductive management in domestic livestock, but remains rare in the captive management of wild animals (Critser *et al.* 2003). An example of nuclear transfer in a wild animal is reported by Lanza *et al.* (2000), who successfully cloned a calf from a gaur *Bos gaurus*, a species of wild cattle; the embryo was then transferred to a domestic cow for gestation. As with many cloned animals, however, the calf did not survive for more than a few days after parturition.

9.4.1 Artificial insemination

Before AI can occur, semen must be collected. This is achieved via a variety of means, such as electroejaculation, manual stimulation/massage (easier and safer in birds than in large mammals), provision of a 'dummy' female with an artificial vagina, or 'cooperative ejaculation' (falconers, for example, use sexually imprinted birds trained to copulate voluntarily on special devices (Hammerstrom 1970)). In mammals, at least, viable sperm can be obtained up to 24 hours after the death of an animal, provided that the testes are kept cool. This has obvious benefits in the case of the unexpected death of a genetically valuable animal from an endangered species. Once collected, sperm (semen) may be used immediately or preserved by freezing (cryopreservation) for future use. Although cryopreservation of sperm is now widespread in farm animal reproduction and in the treatment of human fertility problems, the success of this technique for wild animals is very variable. Donoghue *et al*. (2003) reported a high degree of variability between even closely related species in sperm tolerance of, for example, rapid cooling.

Obtaining viable sperm is only the first stage in successful AI. Sperm must be introduced into the right part of the female reproductive tract, at the right time in the female's reproductive cycle. Again, there is considerable variability between taxa, and even between related species, and species-specific AI protocols are needed for successful fertilization to take place.

9.4.2 *In vitro*[11] fertilization

In vitro fertilization (IVF) refers to the production of an embryo in culture in the laboratory or clinic, as opposed to ***in vivo* fertilization**, which occurs inside the mother's body (in the case of mammals and birds).

---

[11] The term ***in vitro*** literally means 'in glass' and refers to the production of 'test tube' embryos in the laboratory.

IVF can now be accomplished via the injection of a single spermatozoon into an oocyte. This technique is referred to as 'sperm microinjection'. The first mammalian offspring produced in this way were laboratory animals, such as mice and rabbits, using a technique now referred to as 'sub-zonal insemination' (SUZI) (Mann 1988), in which a spermatozoon is inserted just inside the outer coating (zona pellucida) of an oocyte. A development of this technique, which is now more commonly used, involves the injection of a spermatozoon into the cytoplasm of the oocyte. This is known as 'intracytoplasmic sperm injection' (ICSI) (**Fig. 9.17**). ICSI offspring have now been produced in a number of primate species, including humans (for a review, see Loskutoff 2003).

9.4.3 Embryo transfer

Whether produced *in vitro* or as a result of *in vivo* fertilization, there have been a number of cases in which embryos from wild mammals have been transferred successfully into a different species for gestation. For example, Pope (2000) documents
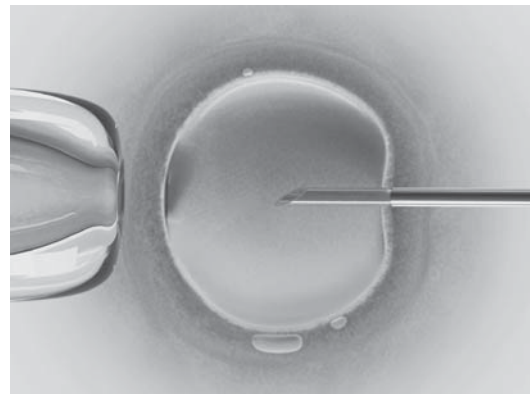
Figure 9.17 This photograph shows intracytoplasmic sperm injection (ICSI), a technique that was developed in 1992 in Belgium. Here, the egg is being held in place by a pipette while a single sperm is injected into the egg using a tiny needle, so that fertilization can occur. ICSI is a particularly useful assisted reproductive technology (ART) when males have a very low sperm count or low sperm motility. (Photograph: © Kiyoshi Takahase, **www.iStockphoto.com**)

this form of surrogacy in two endangered felid species—the Indian desert cat *Felis silvestris ornata* and the African wild cat *Felis silvestris lybica*—from which embryos were transferred into domestic cat surrogate mothers and living offspring produced. Other zoo species in which successful surrogacy has been documented include the gaur (via domestic cattle), the bongo (via an eland), and Grant's zebra and Przewalski's horse (via the domestic horse).

However, Loskutoff (2003) points out that there have been many failed attempts at embryo transfer from wild to domestic species, and that most wild animals do not have an appropriate domestic animal species to act as a surrogate host, so the potential of embryo transfer to help zoos to breed endangered species remains limited, at least for the present time.

9.4.4 The advantages and disadvantages to zoos of using ARTs

The advantages of ARTs

There are a number of advantages to zoos of using techniques such as AI. These can be summarized as follows.

- Logistical facilitation of breeding:
  - transferring sperm or embryos between zoos is cheaper, easier, and safer than moving live wild animals, and also has welfare benefits, in avoiding the need for the sedation, capture, and transport of live animals;
  - the use of ARTs avoids the risk of fighting and injury during the introduction of a male and female for mating;
  - genetic material can be exchanged between *in situ* and *ex situ* populations without the need for the transport of live animals.
- Manipulate the genetic representations of 'valuable' animals within the population:
  - nuclear transfer (cloning) offers the possibility of producing several identical offspring from genetically valuable animals;

- additional offspring can be obtained from a 'valuable' female by using embryo transfer and surrogacy, offering the potential for rapid population growth;
  - offspring can be produced from genetically suitable animals, which are otherwise incompatible, or where there are physical blocks to natural reproduction.
- Manipulate the outcome of breeding attempts:
  - the sex ratio of offspring can be manipulated, either by flow cytometric sorting of sperm, or by the selection of an embryo of the desired gender prior to implantation, helping zoos to overcome the problems associated with surplus males in a population (for example, most zoos have a 'bachelor paddock' housing male animals that would fight if they were allowed to remain within the main social group);
  - the risk of disease transmission from parent(s) to offspring can be reduced by screening of semen for **pathogens** and/or by embryo screening prior to implantation;
  - some developmental abnormalities can also be avoided by use of embryo screening.

The disadvantages of ARTs

The use of ARTs in captive management of zoo animals will undoubtedly continue to grow as the techniques are refined and developed, and as protocols are developed for a greater number of species. But there are two major caveats about the use of ARTs for wild animals:

- there is enormous variability in the success of these techniques across species and taxonomic groups (for example, ICSI does not appear to be very effective in bovid species);
- the use of ARTs has been linked to a range of problems, such as an increase in fetal and chromosomal abnormalities, and a higher rate of spontaneous abortions.

Loskutoff (2003) provides a review of the successes and failures of these techniques, and warns

Box 9.5   THE FROZEN ZOO

It is unlikely that there will ever be many visitors to a 'frozen zoo', but freezing genetic material from animal and plant species, at very low temperatures, represents a technically viable method for helping to conserve species biodiversity, without having to maintain large captive populations of each organism. The principle behind the so-called 'frozen zoo' is to preserve samples of sperm, oocytes, or embryos—particularly from endangered animals—which, with the appropriate technology, could be used in the future to contribute to maintaining genetic diversity in breeding programmes (Holt *et al.* 2003). This storage of gametes or embryos is also known as 'genetic resource banking', and efforts by zoos and other organizations to establish genetic resource banks (GRBs) have now been in place for more than 50 years.

Freezing gametes (and other material) at very low temperatures (typically −196°C, or −321°F) is known as cryopreservation. Techniques for freezing spermatozoa were developed more than 50 years ago, with pioneers such as Sir Alan Parkes leading the way in the newly emerging field of cryobiology (Watson and Holt 2001).

Vertebrate eggs or oocytes (called ova when mature) are more difficult to cryopreserve successfully than spermatozoa, or even embryos, and even with recent technological advances in this field, the successful cryopreservation of vertebrate oocytes remains a challenge.

The Frozen Ark Project, set up in 2003, is a worldwide initiative to collect, preserve, and store both DNA and, where possible, gametes and embryos, from threatened species of animal (see **http://www.frozenark.org**). Currently coordinated from the University of Nottingham in the UK, the Frozen Ark's list of consortium members includes the Natural History Museum in London, the Zoological Society of London (ZSL), Monash University in Melbourne, Australia, and many other universities, zoological societies, and conservation organizations from around the world.

Cryopreserved gametes can be regarded as genetically equivalent to living animals, with the advantage that they will provide valuable genetic material for years to come without the threat of the genetic loss that can occur over generations when living animals are bred.

---

that much more research is needed to develop effective protocols for non-domestic species.

Similar caveats apply to the successful freezing or cryopreservation of sperm, in relation to which even related species show considerable differences in tolerance of freeze–thaw procedures (Donoghue *et al.* 2003) (see **Box 9.5**).

9.5 Rearing: facilitating the successful survival of offspring

In the earlier sections of this chapter, our focus has been on the physiological and behavioural basis of reproduction, with special emphasis on mating behaviour and conception. In this section, we will consider rearing (**Fig. 9.18**) and review how the

survival of any offspring that hatch or are born can be enhanced through husbandry. This starts with a look at the prudence of ensuring that adequate facilities are made available to animals prior to their giving birth or laying and protecting eggs, and then when the offspring hatch or are born.

There are potentially many reasons why zoo professionals may feel that it is necessary to intervene with the rearing process. Usually, this is when rearing does not appear to be going well, but intervention may also occur to ensure or artificially increase rearing success. Interventions can be broadly divided into those that leave the offspring in the social group, so that the keepers provide supplementary rearing, and those that involve removing the offspring from the social group. Equally, it is necessary that precautionary

Figure 9.18 Within the animal kingdom, the degree to which parents care for and rear their young is highly variable, although it is common for many mammal and birds species to invest considerably in rearing young, depicted here by (a) babirusa *Babyrousa babyrussa* and (b) bison *Bison bison*. (Photographs: (a) South Lakes Wild Animal Park; (b) Carlos Freij, Berlin Zoo)

steps are in place prior to parturition or hatching, just in case there is a hitch.

Of course, for a great many species—especially amphibians, fish, and some reptiles—the process of rearing by the parents can be extremely limited and sometimes non-existent. Eggs are laid, the parents leave, and the survival of offspring is then dependent on their own abilities to survive. In zoos, ensuring the survival of these offspring is sometimes simpler than for those that require rearing, because they can often be provided with the appropriate feeding and climatic conditions, and they then survive to become reproductively competent adults. But the survival and long-term success of animals that require, but do not receive, adequate rearing from their parents can be severely compromised. The outcome of providing supplementary or full-time artificial rearing by keepers is variable (see **Box 9.6**).

9.5.1 Providing adequate facilities

Zoos should provide animals with conditions that best enable them to rear their offspring

successfully. Identifying the optimal conditions for any situation is always a difficult task, so it may be more constructive to consider what animals need in three stages: when pre-partum or gravid, post-partum or post-lay, and during rearing.

Animals' needs can be assessed in a variety of ways, as outlined in **section 7.2** (**Fig. 9.19**). Prior to and during rearing, it is likely that the factors affecting the animals' ability to rear their offspring will include the health (including nutritional demands) of the parent and offspring, and housing and husbandry facilities. Zoos should attempt to identify the needs of the animals and what behaviours they might need to express during the three stages of rearing offspring, and ensure that the appropriate conditions are provided. It is also important to make efforts to ensure that the artificial nature of living in a zoo environment does not compromise the animals or restrict their behavioural expression during these stages.

Currently, much of the general practice implemented for gravid or nesting animals is informed not by empirical data, but by intuition or anecdotal information, based greatly upon 'tradition' and

Figure 9.19 Given the opportunity, many animals in zoos will breed successfully, as here in (a) Javan brown langur *Trachypithecus auratus* and (b) red-crowned crane *Grus japonensis*. (Photographs: (a) Joy Bond, Belfast Zoo; (b) Paignton Zoo Environmental Park)

'word of mouth'. Some of these practices make perfect sense and do not require empirical support—for example, the separation or removal of eggs or young animals that are in danger of being eaten by their parents or by other conspecifics or heterospecifics housed in the same enclosure. More debatable, however—and probably variable among individuals and species—is the need for privacy during mating, laying, or parturition. Anecdotally, it has been noted that many zoo animals give birth at night, or at least outside visiting hours, which has been interpreted as a choice for 'quieter' conditions, although many wild animals also give birth at night and this may be related to predation pressures (Rowland *et al*. 1984).

For some animals that seem especially sensitive to disturbance, some routine husbandry procedures (for example, periods of human–animal interaction, when keepers may enter the animals' enclosure for cleaning, or viewing of the animals by zoo visitors) may be delayed for a short time around parturition or egg-laying. The extent to which animals are susceptible to disruption is a topic that has received little attention from researchers, even though, in a captive environment, it is very likely to influence reproductive success, among other things, (see **section 7.3.1** and **Fig. 9.20**). However, there are data that highlight the need to increase the food availability to gravid and lactating animals (see **section 12.4**) and that provide some information about what constitute appropriate nesting materials or structures for some species.

9.5.2 Supplementary parenting

In some circumstances, it is possible to facilitate rearing without the need to take offspring away from their parents or social group. This may simply require that some alterations are made to the routine housing and husbandry of the animals, such as food being chopped up smaller for weaning offspring.

Figure 9.20 Providing animals with the appropriate conditions is fundamental to stimulating reproduction, which can be achieved by providing appropriate nesting conditions, as for these hyacinth macaws *Anodorhynchus hyacinthinus* (a), or areas within the enclosure that provide privacy for the offspring, which was accommodated by long grass for this baby pudu *Pudu pudu* (b), all of which will hopefully lead to successful births, such as this shoebill *Balaeniceps rex* born in Parc Paradiso (c). (Photographs: (a and b) Paignton Zoo Environmental Park; (c) Jeroen Stevens, Parc Paradiso, Belgium).

Alternatively, more dramatic interventions can be undertaken to supplement rearing directly. For example, keepers can provide additional food to infants, train animals in parental skills, and undertake health checks and diagnostics on infants without the need to handle them directly (Desmond and Laule 1994). These and other steps, termed 'supplementary parenting', have been shown to promote the survival of offspring without the intervention of removal of the offspring.

9.5.3 Removing offspring from their parent and/or group

To many people, the removal of offspring from their parents would be seen as a last resort and would only be carried out if the survival of the parent or offspring were in doubt. This might result from inappropriate housing and husbandry, or from ill health or poor parenting skills. For example, Buckanoff *et al.* (2006) noted that the high level of neonatal mortality in pottos *Perodicticus potto* is probably largely due to inadequate maternal behaviour, and thus hand-rearing attempts have been made (**Fig. 9.21**). As discussed above, it can take several attempts to appreciate fully and to identify the housing and husbandry facilities that are necessary to enable parents to rear their offspring. This might be thought of as a gap in the abilities of zoos, but really it is not surprising, given the large number of species that zoos attempt to breed in captivity.

However, there are some circumstances under which the removal of offspring from their parents is part of planned captive management. The most notable argument for such an action is to increase the number of offspring produced. In **section 9.6.1**, we will discuss the practices of **double-clutching** and decreasing inter-birth interval as methods used to increase population size. Both of these techniques require that the offspring are removed and reared independently of their parents.

When and for how long an offspring is removed from its parents is highly variable and dependent on the end goal. If offspring are removed with the sole aim of hand-rearing, they will obviously remain away from their parents for the duration of rearing. However, if removal has been undertaken as a mitigating step to try to ensure survival of either the parent or offspring, then the two could be reunited very quickly indeed; eggs may be removed from some birds and incubated, and then the chicks returned to the parents after hatching. Similarly, problems around the time of birth can be resolved with some immediate and short-lived intervention from keepers, which enables them to get the offspring back to its parents in a very short period of time. Certainly, documentation of successful hand-rearing events has demonstrated that offspring can be successfully reunited with parents (Abello *et al.* 2007). However, it should be noted that there are a great many factors that determine the success of these reunions, including the social group size and composition, enclosure design, personalities of the animals, and much more.

When offspring are taken away from their parents, the decision of who takes over the role of rearing is determined by the availability of appropriate surrogates and facilities, and the offspring's age (for example, do the offspring still require milk or are they weaned?). It might also be possible for slightly older animals to forgo the surrogate mother and be grouped socially with peers, and have any additional needs met through some supplemental parenting from keepers. Surrogate mothers can be animals of the same or different species, including people, who are usually keepers. For example, domestic chickens have been used for many years to incubate and rear chicks from game birds and waterfowl species (Sutherland *et al.* 2004).

Whether animals should be taken away from their parents for rearing is a contentious topic both within and outside the zoo profession. Consider, for example, the discussion and media attention that was attracted by the particularly charismatic Knut, an abandoned polar bear cub, that was hand-reared at Berlin Zoo. But clarity is required—rarely

Figure 9.21 Hand-rearing is the most common and successful method of breeding many species of bird and reptile in captivity, but the topic of hand-rearing mammals is often seen as much more controversial, with many zoo professionals split over whether hand-rearing should or should not be undertaken. For some species, the alternative is something that is almost as unacceptable. (Photographs: (a and b) Paignton Zoo Environmental Park; (c) Dave Rolfe, Howletts)

Box 9.6 HAND-REARING

Whether or not zoos should hand-rear animals is a controversial topic. But it is probably safe to say that much opinion about hand-rearing, and certainly the research undertaken to monitor its impact, is biased towards mammals (e.g. Ryan *et al*. 2002). Published literature about hand-rearing other taxa is available, but these are usually methodological practical papers (for example, on the Anegada island iguana *Cyclura pingluis* (Lemm *et al*. 2005)). This is true of many topics that we have discussed in this book, but the importance of highlighting the species bias in hand-rearing is considered standard, and not at all controversial, for many reptile, amphibian, and bird species that would not necessarily gain much parental care in the wild, but which require it in zoos. It is possible that the degree to which hand-rearing will have negative implications, if indeed it has any, will be greater for offspring that are more heavily reliant on their parents and whose **survival skills** and behaviours are formed during this period.

There are three main reasons why a young animal might be removed from its parents and hand-reared, which can best be summed up as providing an advantage to one of three different parties: the young animal—if neglected by its parents and still dependent on their care, it may die or suffer without appropriate attention; the species—the removal of offspring may trigger breeding and increase the population size more quickly compared with natural breeding (double-clutching); the zoo professionals—the process of hand-rearing requires skills that are most effective with practice.

It should also be noted that, in the recent past, animals may also have been hand-reared as a visitor attraction, but this is less common and certainly not usually considered nowadays as the primary reason for hand-rearing.

So why should hand-rearing be considered bad? Many animals appear to thrive during hand-rearing and as adults, but there are notable exceptions within the mammalian taxa and among some bird species, in which disruption of the mother–infant bond appears to have deleterious ramifications (Cirulli *et al*. 2003). Hand-rearing has been reported to result in behaviourally incompetent animals, which is observed as animals that are unable to communicate effectively or to behave normally with conspecifics; this has far-reaching ramifications, because it potentially compromises their long-term social interactions and breeding contributions to the population (Martin 2005). One of the main disadvantages of hand-rearing occurs as a consequence of **imprinting** on the human care-giver, whom the animal then recognizes as a conspecific. This can be partly overcome by, for example, modifications to hand-rearing protocols, which have included the use of puppets to conceal the identity of the keeper (Valutis and Marzuluff 1999) (see also **Fig. 10.15**).

And what if zoos do not hand-rear animals that are rejected by their parents? The answer is simply that they have a duty of care to **euthanize** them, rather than to allow them to die 'naturally', because this will limit any pain or suffering.

---

are the issues of the utility of incubators to facilitate bird and reptile reproduction, or, in fact, methods used to increase the populations of these taxa, discussed. Instead, the controversy is usually about the use of hand-rearing for zoo animals, and especially the hand-rearing of mammals (see **section 10.4.5** and **Fig. 10.15**)

A summary of some of the costs and benefits associated with hand-rearing is presented in **Box 9.6**.

9.6 Manipulating exotic animal reproductive output

Carefully planned captive management programmes use demographic and genetic analyses to produce long-term projections and goals for the species. Goals made for a captive population will include whether attempts should be made to increase or decrease its size, or to keep

the population size stable (see **Box 9.7**). There are various mechanisms that can be used to modify population size and these are reviewed in the next two sections. Any changes made to the size of the population need to be implemented with caution and with consideration of the genetic goals of the captive management programme. These, as explained in **section 9.2.2**, usually aim to maximize genetic diversity and avoid inbreeding. Because of this, taking steps to change the population size needs to be coordinated between all the zoos holding the given species and thus is usually managed by captive management coordinators as part of an authorized programme (see **sections 9.7.2** and **9.7.3**).

9.6.1 Increasing reproductive output

'Reproductive output' refers to the number of offspring born. There are two main ways in which this can be relatively easily increased. In egg-laying species, this is through a process termed double-clutching; in mammals, this can be achieved by reducing the **inter-birth interval** or by decreasing the age at which animals have their first offspring.

Double-clutching

Some egg-laying species have been observed to lay more than one clutch in a breeding season. Double-clutching is undertaken in zoos in the hope that this will stimulate the animal to lay another clutch and thus double its reproductive output. For example, Woolcock (2000) comments that successful breeding attempts with keas *Nestor notabilis* at Paradise Park in the UK are largely due to the removal of eggs that have been incubated. In this case, one female laid twenty-two eggs in a 12-week period, which obviously increased her reproductive potential and accelerated population growth.

Reducing the inter-birth interval

Anecdotally, it is assumed that inter-birth intervals have become shorter and that the age of first birth has decreased in zoo-housed mammals, as an unintentional consequence of housing and husbandry. It has generally been thought that reducing these two parameters will also increase the overall fecundity and fertility (reproductive output) of animals. Only recently has the impact of changing these life history strategies been investigated empirically.

Cocks (2007) reviewed various life history traits in the zoo population of orang-utans and discovered that when the age of first birth and inter-birth interval were shortened, compared with the ages at which these events are observed in the wild, the **longevity** of the animals was also shortened, so that mortality was earlier. Because there are so few data available on this topic, it is difficult to know whether these results reflect a trend that changing life history variables in captive mammals is deleterious, or whether orang-utans are an exceptional case. But it is certainly an area that requires greater research.

9.6.2 Reducing reproductive output

It may seem counter-intuitive that methods of reducing reproductive output in zoo animal populations is necessary but, as outlined in **Box 9.7** and **section 15.5.1**, many captive management programmes may have limitations imposed on them, requiring that they do not increase populations, but maintain them at stable levels, or, indeed, reduce them over time.

There are various way in which this can be achieved, the simplest of which is to separate the sexes and maintain groups of singly-sexed animals. This approach has been adopted for several species, including Rodrigues fruit bats *Pteropus rodricensis* and red-ruffed lemurs *Varecia rubra*. Another simple, but controversial, method is to operate a system termed **breed and cull**. This strategy allows animals within the population to breed, as normal, but resulting offspring are culled. The number and age of animals which are culled can vary depending on the animals' life history strategy, social group composition, and space availability. Both these strategies can be implemented simply and easily. There are potentially

greater complications in separating sexes than there are in culling offspring, because single-sex groups are not necessarily part of the natural social systems of the species for which this strategy is attempted. Conversely, allowing adults to have offspring enables them to express many of their naturally occurring behaviours, and so could be thought of as an ideal management tool, if viewed from the perspective of the behavioural needs of the adult animals (see **Box 7.4**).

The other main method used to reduce reproductive output is the use of contraception. Various types of contraception are available that operate in different ways—for example, by preventing ovulation or the implantation of a fertilized egg. They act on the reproductive biology of either the male or female animal, and thereby ensure that no offspring are born. Contraception can be achieved through physical separation, surgical techniques, and manipulation of endocrine function with synthetic hormones. Some of the most common methods are summarized in

Table 9.2. Obviously, if it is likely that an animal might be required to breed in the future, a temporary measure should be chosen. The various methods available are effective through the removal of reproductive organs (or parts thereof), the modification of endocrine control of reproduction, immunization against implantation, and delaying maturation or reducing the survivorship of birds' eggs (the latter is a method used to render eggs unviable).

As use of contraception is becoming more widespread, and its use is being monitored more effectively, it is becoming apparent that it can be associated with deleterious events. To this end, it is very important that the contraception used is monitored and evaluated, so that more can be learnt about its action on a variety of different species. Both the AZA Wildlife Contraception Center and EGZAC (**Fig. 9.22**) offer advice on which contraception method to use, and importantly systematic tracking once contraception has been initiated.

Figure 9.22 The recently established European Group on Zoo Animal Contraception (EGZAC) works to support captive management programmes by adopting an evidence-based approach to contraception, and advice on its use. Like the AZA Wildlife Contraception Center (both parties work together), EGZAC use data gained from surveys to better understand the impact of different contraceptives on a wide range of species. See their webpage **http://www.egzac.org/ aboutus.aspx**

Method	♂/♀	Reversible (duration)	Latency to effectiveness	Surgical	Behavioural effects	Comments
PHYSICAL SEPARATION						
Single-sex group	Both	Yes	Immediate	No	Abnormal social grouping—aggression may occur	May be able to introduce an adult male to an all-female group for short periods for breeding
SURGICAL						
Vasectomy	♂	No	Immediate	Yes	None (that we know of)	Will not reduce birth rate unless all the males in the group are treated, but can reduce breeding by over-represented individuals
Castration	♂	No	Immediate	Yes	May reduce aggression between males BUT only if done before puberty	As for vasectomy
Tubal ligation	♀	No	Immediate	Yes	Normal sexual maturation and behaviour	Specialist surgical technique (keyhole surgery) or laparotomy, with concurrent need for post-operative wound management
Ovarectomy/ hysterectomy	♀	No	Immediate	Yes	Acyclic	Laparotomy required, with concurrent need for post-operative wound management
HORMONAL						
GnRH implants (e.g. deslorelin)	♂	Yes, variable (each implant lasts approx. 2 years) Implants biodegrade and cannot be removed	Highly variable, can take months	Yes	Delays puberty by reducing testosterone levels May not eliminate aggression in post-pubertal males (similar to castration)	Can lead to abortion if used in pregnant females No other known contraindications Further evaluation required to determine optimum dose rate and interval

Method	♂/♀	Reversible (duration)	Latency to effectiveness	Surgical	Behavioural effects	Comments
HORMONAL (*Continued*)						
Progestin implants (e.g. melengestrol acetate, implanon, Norplant)	♀	Once hormone levels drop below threshold, normal reproductive function resumes (cf. Depoprovera)	Up to 3 weeks		Delays puberty Can synchronize seasons May induce a season immediately after implant insertion— should then be acyclic for duration of implants	
	♀	Yes (approx. 2 years) Implants can be removed early to initiate oestrus	2 weeks	Yes	Some individuals may still show a sexual swelling, which does not imply contraceptive failure	Can be used in pregnancy and during lactation Caution: early removal by grooming may occur
Oral progestins (with or without oestrogens)	♀	Yes, should return to normal within 1–2 weeks	1–2 weeks	Yes	If the progestin is used continuously, no swellings will be seen Administration of a week's worth of placebo tablets will lead to signs of oestrus	Can be used in pregnancy and during lactation
Injectable progestins (e.g. Depoprovera)	♀	Yes, in most cases (approx 2–3 months), but it may take up to 2 years for normal cycling to return	2 weeks	Yes	Generally acyclic	Useful for short-term contraception Caution: with consecutive treatments, the ability to predict when normal functioning will return becomes difficult

Table 9.2 A summary of available forms of contraception*

*From Sanderson (2007).

Note: Contraception can be achieved in a variety of ways, as summarized here, although broadly categorized as separating the sexes, so that they do not have access to one another and therefore cannot reproduce, to performing surgery to impair the proper functioning of the reproductive tract, and finally through the administration of hormones, which causes endocrine dysfunction and reproductive failure.

9.6.3 Sex ratios and their manipulation

As described in **Box 9.1**, there are various factors other than genetic make-up and endocrine function that can influence the determination of sex. Although there are few data that have empirically described how these other factors can affect sex ratio determination, some papers have demonstrated that factors such as nutrition, population density, and the social status of the mother can have a significant influence on sex ratio (e.g. Kilner 1998; Loeske *et al*. 1999; Melfi 2012b).

ARTs can be harnessed to manipulate the sex ratio of offspring. Firstly, IVF embryos of the desired sex can be directly selected and implanted. Secondly, AI and IVF can be carried out using pre-sorted sperm, so that only male or only female embryos result. Flow cytometric sorting is a technique for separating the X- and Y-chromosome-bearing sperm of mammals. This is possible because the X chromosome is larger than the Y chromosome, and so sperm carrying an X chromosome are slightly heavier than their Y chromosome counterparts. Flow cytometric sorting of sperm is now widely used in farm animal production (for example, to produce cows, rather than bulls, for the dairy industry (see Johnson 2000)), but is not yet common in wild animal reproduction.

9.7 Working towards self-sustaining populations in captivity

If the number of births and deaths in a captive population can be balanced, and the overall population kept stable, it would be considered demographically self-sustaining—a target to which captive management programmes aspire. More difficult to achieve is genetic self-sustainability; unfortunately in a closed system such as a captive management programme it is inevitable that some genetic diversity will be lost over time (Lacy 2013). Using different measures of self-sustainability Magin *et al*. (1994) estimated that, although zoos worldwide held 34 per cent of all threatened mammal species, only half of these (17 per cent) could be considered to be part of a self-sustaining population. Another analysis (WRI 1992) suggested that, of 274 species then listed in captive management programmes, only twenty-six were self-sustaining in captivity. Although the numbers differ between these papers, the trend is the same—zoos maintain few recognized threatened species, and those that are housed in zoos may not be there for the future, because they are not being managed as part of self-sustaining populations.

In this final section, we will consider the decision-making processes used to determine which species should be maintained in zoos. The infrastructure that underpins the captive management of zoo-housed species is very similar in the different regional zoo and aquarium associations, and is overseen by **Taxon Advisory Groups (TAGs)** that manage different levels of captive management programmes. The ultimate goal of these programmes is to increase, decrease, or keep stable the captive population for a given species, and this inevitably requires manipulations to strive for populations that will be self-sustaining (see **Box 9.7**).

9.7.1 Should the species be maintained in zoos?

Captive management programmes are coordinated regionally and globally, through regional zoo associations (European Association of Zoos and Aquaria (EAZA), Association of Zoos and Aquariums (AZA), Zoo and Aquaria Association (ZAA), etc.) (see **Chapter 3**) and the World Association of Zoos and Aquariums (WAZA).

Within regional zoo associations, groups of specialists form Taxon Advisory Groups (TAGs), which review, assess, and recommend which animals should be held in zoos in that region. The membership of a TAG will include a chairperson, possibly a vice chairperson, the coordinators for each captive management programme, and invited specialists, such as advisers on genetics, nutrition, and veterinary research. The number of species included within each of these TAGs is highly variable. For mammals and birds, the TAG

Box 9.7   TO BREED OR NOT TO BREED?

The goal of good zoos is to conserve species through self-sustaining captive populations, which might require captive breeding or restrictions placed on breeding. We have mentioned at several points throughout this book that there are limited spaces available within zoos to hold animals and yet, to manage a successfully self-sustaining population, a large number of animals are required.

It has been suggested that zoos worldwide might need to support the captive management of 2,000 vertebrate species (Soulé *et al*. 1986), but more recent estimates for specific taxa have suggested that there are only enough spaces in the North American zoos for self-sustaining populations of 141 bird species (Sheppard 1995) and sixteen snake species (Quinn and Quinn 1993). Therefore decisions are made to prioritize which species should be maintained and managed with different regional zoo associations (for example, the European Association of Zoos and Aquaria (EAZA)—see **section 9.7.1**), and whether these populations should be increased, kept stable, or decreased (see **section 9.7.3**).

Common reasons why a species will be managed and bred in captivity include the following.

1. The 'ark principle', whereby the captive animal represents a 'safety-net population' for an endangered species. The long-term goal of these populations is that they could be reintroduced to ameliorate wild extinctions and also to reduce the pressure on wild populations as a source of animals for other captive situations. However, after its initial conception this principal received a lot of critism, with a return to a focus on species conservation; the ark principle is still considered to have value (reviewed by Bowkett 2009) (see **section 10.7**).

2. Allowing animals to breed also provides them with the opportunity to show their full behavioural repertoire, including courtship and parental care.

3. The very powerful attraction that baby animals offer to the public is likely to attract additional numbers of visitors through the gate.

may operate at order, family, or even genus level (for example, 'deer' or 'hornbill'), or may be more general (for example, 'marine mammals'). Aside from these, it is not uncommon for many disparate species and/or taxa to be grouped where few or any animals or little knowledge exists; for example, within EAZA many animals are bought together under the three TAGs 'terrestrial invertebrates', 'fish and aquatic invertebrates', and 'amphibians and reptiles'.

Regional collection planning

A key role of TAGs is to develop and manage **regional collection plans (RCPs)**, which aim to identify whether species should be managed and consequently make recommendations to zoos about the species that they should aim to incorporate in their collections.

As an example, Wilkinson (2000) provides an overview of the activities of the EAZA parrot TAG. He highlights that, of about 130 parrot species classified as threatened or endangered, only a handful of EAZA captive management programmes exist and five international **studbooks** are maintained that aim to coordinate efforts between zoo associations. A lot of information is gathered and discussed by TAGs in order to create regional collection plans and make the necessary decisions to achieve self-sustaining populations, including, but not limited to, current captive population, potential capacity for captive population, value to conservation, research, education, or exhibition, inherent uniqueness within the taxon, and the likelihood that populations can be managed successfully and be self-sustaining. These can be influenced by various factors, such
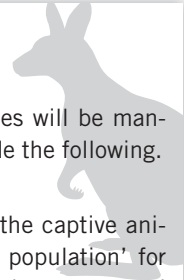
as space availability, previous breeding success, and genetic parameters (for example, genetic diversity and inbreeding coefficients of the population).

Three main decisions can be made on the basis of this information: to manage the species as part of a captive management programme, which could operate at a series of different levels; to phase out the species; or to gather more information before a final decision is reached. Reaching a decision for each species is complicated, because it relies on information about other species within the TAG. For example, all species of gibbon are considered in danger of extinction (Geissmann 2007), so when space for exhibiting gibbons in zoos is limited, factors other than the conservation value of the different species need to be considered when planning which species zoos in that region should hold.

To facilitate this process, some TAGs have developed decision trees to help them to maintain some consistency and logic when choosing whether a species should be included in the RCP. The most common reason why a TAG would recommend that a species should not be managed or held in zoos is that space is limited and that another species is considered to take precedence, because it is more endangered. Alternatively, if the captive population for a species is very low and would require supplementation from wild stocks to ensure its survival in captivity, unless there were extreme circumstances it is unlikely that it would be recommended for captive management. The removal of animals from the wild to restock captive populations has been undertaken in extreme circumstances, but is not a practice that is undertaken lightly.

Once it has been decided that a species should be maintained in the region's zoos, it is sensible that this is managed by a captive management programme.

9.7.2 Levels of captive management

It is clear that the captive management of species requires coordination between many zoos and cannot be achieved by individual zoos operating alone (**Fig. 9.23**). The concept of metapopulations and the genetic management of captive populations relies on cooperation between zoos, including the exchange of animals for breeding purposes where necessary—and this is a large and complex undertaking.

Although various different terms are used to describe management programmes in different zoo associations worldwide, the underlying goals and the mechanisms used to achieve these are nevertheless very similar. **Table 9.3** outlines the main captive management programmes that exist in three of the regional zoo associations (EAZA, AZA, and ZAA). Some programmes are also coordinated at an international level, via international studbooks. More recently, WAZA have also introduced Global Species Management Programmes, which aim to unify efforts between regions and the habitat country from which the species originates, integrating *ex situ* and *in situ* conservation activities; thus far only a handful of these have been sanctioned, representing two programmes for the AZA, EAZA, and ZAA region, for species such as the okapi *Okapia johnstoni* and red panda *Ailurus fulgens* (Lees and Wilcken 2009; 2011).

A bewildering variety of names and acronyms are used to describe these programmes: European endangered species plans (EEPs)[12] and European studbooks (ESBs) in the EAZA region; green and yellow species survival plans (SSPs) and red population management plans in AZA; and in ZAA member zoos they collaborate in population management plans (those which are organized through a government agency are referred to as conservation management plans). Then there are management or preservation programmes

---

[12] EEPs are colloquially referred to as **European endangered species programmes**, because the acronym is taken from the German *Europäisches Erhaltungszuchtprogramm*; they should not be referred to as EESPs. The first six species to be managed this way were the Congo peafowl, red panda, tiger, bearded vulture, okapi, and Malayan mousedeer.
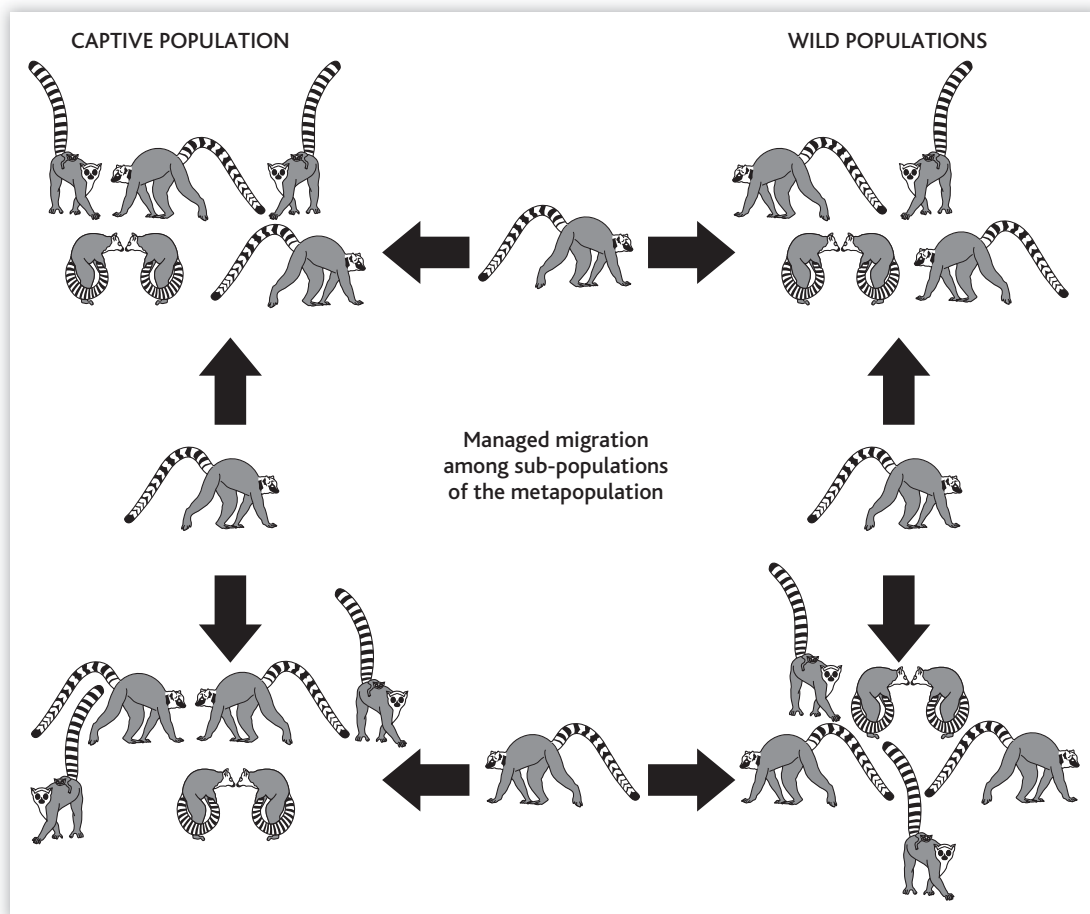
Figure 9.23 A metapopulation describes a situation in which there are several breeding sub-groups, between which individuals will sometimes move. This is exactly how captive management programmes operate, with each of the zoos representing a breeding sub-group and the regional management programme serving as the mechanism through which to move animals between sub-groups/zoos.

elsewhere in the world, and those populations which are simply monitored.

Table 9.3 summarizes the main species management programmes implemented through AZA, ZAA, and EAZA. There are differences between the regional associations in the number of TAGs, because of the size of the region, historical holdings, and legal restrictions (or otherwise) related to animal moves. Some of the key acronyms are summarized and explained in **Table 9.4**.

Collaborative captive management programmes

Using EAZA member zoos as a reference point, it is easy to see that collaborative captive management programmes are diverse and vary from one another in the intensity with which they are managed. An EEP is the most intensive captive management plan. Each EEP has a species coordinator and a studbook keeper (these first two positions are sometimes held by the same person), and they are assisted by a species committee and species advisers, who are specialists in various fields, such as nutrition, research, veterinary, and education. They are thus much like a TAG, but dedicated to one species rather than a group of species.

Any zoo that is an EAZA member, and holds a species for which there is an EEP, instantly becomes part of, and is required to cooperate with, that management programme. Each year, a studbook should be produced which provides a summary of the captive population held in EAZA

	AZA (Association of Zoos and Aquaria) Established 1924		ZAA (Zoo and Aquaria Association) Established 1991			EAZA (European Association of Zoos and Aquaria) Established 1988	
Taxon advisory groups	47		9			41	
Captive breeding programmes	SSP: Green = 35; Yellow = 283; Red = 274*		CMP: 24	PMP: 60	Mon: 28	EEP: 188	ESB: 190
Date initiated	1981	1994				1985	
People involved	Species coordinator and committee	Population manager/ studbook keeper				Species coordinator and committee	Studbook keeper
Collect data: births/deaths/ moves	✓	✓	✓	✓		✓	✓
Analyse data	✓	✓	✓	✓		✓	✓
Produce studbook	✓	✓	✓	✓		✓	✓
Recommend moves/mates	✓	(✓)	✓	✓		✓	(✓)
Construct long-term management plan	✓	(✓)	✓	✓		✓	(✓)
Housing and husbandry guidelines	✓		✓	✓		✓	
Link with *in situ* conservation	(✓)		✓	(✓)		(✓)	

Table 9.3 A summary of the capture management programmes of AZA, ZAA, and EAZA

Note: There are many similarities in the ways in which captive management programmes are organized between different regional zoo associations, as illustrated here for three of the regional zoo associations, in Australasia (ZAA), Europe (EAZA), and North America (AZA).

*As this system is new, programme assignment is still under review.

Acronym	Full name	Area of operation	Other information
CBSG	Conservation Breeding Specialist Group	Worldwide Operates via the IUCN	Formerly Captive Breeding Specialist Group
CP	Conservation programme	ZAA (Australasian region)	ZAA also operates PMPs
IUCN	International Union for the Conservation of Nature and Natural Resources	Worldwide	Better known as the World Conservation Union
RSG	IUCN/SCC reintroduction specialist group	Worldwide Operates via the IUCN's SSC	One of the IUCN/SSC specialist groups
SSC	IUCN Species Survival Commission	Worldwide Operates via the IUCN	Produces the IUCN Red List of Threatened Species
WZCS	*World Zoo Conservation Strategy* (1993)	Accredited zoos worldwide	Produced as a joint initiative between WZO and IUDZG, and CBSG/IUCN/SSC
WZACS	*World Zoo and Aquarium Conservation Strategy* (2005)	Accredited zoos worldwide	Published under the title *Building a Future for Wildlife* Also developed jointly with the IUCN, CBSG, and SSC

Table 9.4 A summary of some of the key acronyms used within the zoo and conservation industries

Note: For a comprehensive list of acronyms relating to conservation initiatives and programmes, both within and outside zoos, see the AZA website (**http://www.aza.org**).

member zoos, and highlights any births, deaths, and transfers that have occurred during that year. On the basis of the information held within the studbook, genetic and demographic analyses are undertaken, based on which recommendations are made to all EEP members in relation to whether any of their animals are permitted to breed or need to be transferred to other zoos for breeding.

European studbooks (ESBs) are less intensively managed programmes that essentially monitor the captive European population for a given species—that is, whether it is increasing, decreasing, or remaining stable.[13] Studbook keepers for each ESB can advise on which animals should be exchanged with other zoos, but their advice is not binding on participating zoos in the same way that recommendations from an EEP species coordinator are.

Finally, some species are managed in monitoring programmes, in which there is no established requirement other than that a person is designated to take a 'special interest' in a species; no studbooks need to be generated.

It should be noted that other regional zoo associations also operate and have similar infrastructure to that described here. Some of these associations are still relatively young, small, or diverse in their membership, which makes coordinating these collaborative captive management programmes

---

[13] New international studbooks can only be set up with the approval of WAZA and the IUCN/SCC. Global Species Management Programmes (GSMPs) which aim to integrate more fully all aspects of the *in situ* and *ex situ* conservation of a species are currently being initiated.

challenging. For example, the African Association of Zoos and Aquaria (PAAZAB) initiated African Preservation Programmes (APP) in 1991 and now administers twenty regional studbooks.

Classification of collaborative captive management programmes

All zoo regions operate collaborative captive management programmes at different levels of intensity, but the criteria used to determine this classification are variable. AZA member zoos classify the intensity of their programmes according to the degree to which they believe the captive population can be considered sustainable. 'Green' programmes represent populations of over fifty individuals from which 90 per cent genetic diversity can be sustained over 100 years. 'Yellow' programmes represent populations of over fifty individuals that may not be able to maintain 90 per cent genetic diversity over 100 years. 'Red' programmes represent populations of less than fifty individuals in which genetic diversity cannot be sustained. In contrast, the level of intensity used to manage programmes by EAZA member zoos is more flexible; for example, they can be determined by conservation status (i.e. for critically endangered species) or management need (i.e. to control the size of populations by supporting growth, decline, or stability). In a recent paper by Hogg *et al.* (2012), which described programmes operated by ZAA member zoos, the authors worked retrospectively by considering whether the current programmes were able to achieve preset goals and short-term sustainability. Thus, they categorized their programmes according to a set of criteria, which were not limited to population criteria, but also included considerations about how well the programme was administered, and which resulted in the following classifications: green—excellent; orange—good; red—weak.

9.7.3 Balancing births and deaths with varied lifespans and litter sizes

In order to create a stable self-sustaining population in which the number of animals remains constant, the number of animals that are born

and die each year must be equal. If, on the other hand, the aim is to create a growing population, the number of births that occur yearly should surpass the number of animals that die yearly. There are obviously many variables that affect how many animals are born or die in a year, but in a well-organized captive management programme, some of these variables can be controlled by housing and husbandry and by other strategies adopted by zoos (see **section 9.7.4**).

Which strategy is adopted will, to some extent, be determined through analyses of the data held within studbooks. By looking at the historical population dynamics for a species, it is possible to determine what level of births (fertility) and deaths (mortality) can be expected annually. For example, if you look at **Fig. 9.24**, which illustrates the fertility and mortality of the animals in the Sulawesi crested black macaque *Macaca nigra* EEP, you can see that the rate of births far outweighed the number of deaths in the population (calculated from the historical data recorded over more than 30 years). These data demonstrate that this species can be maintained as a growing population, when considering the number of animals alone. But this information does not provide an indication of the genetic value of the population.

The ease with which a self-sustaining population can be managed to ensure that it has a high genetic diversity and low inbreeding depends on several life history traits, including the animals' longevity, inter-birth interval, and litter size. Good examples of the type of information that can be gleaned about captive populations are presented by Marker-Kraus (1997) and Blomqvist (1995), who provide information about how the captive cheetah *Acinonyx jubatus* and snow leopard *Panthera uncia* populations have changed over some 30 years. During this period, the snow leopard management programme has increased from ten in member zoos in 1961 to 160 in 1992, 98 per cent of which are captive-born (Blomqvist 1995).

It is more difficult to manage genetically short-lived species and those that have a large number of offspring, compared with longer-living species or those that have few offspring. Morton (1990)
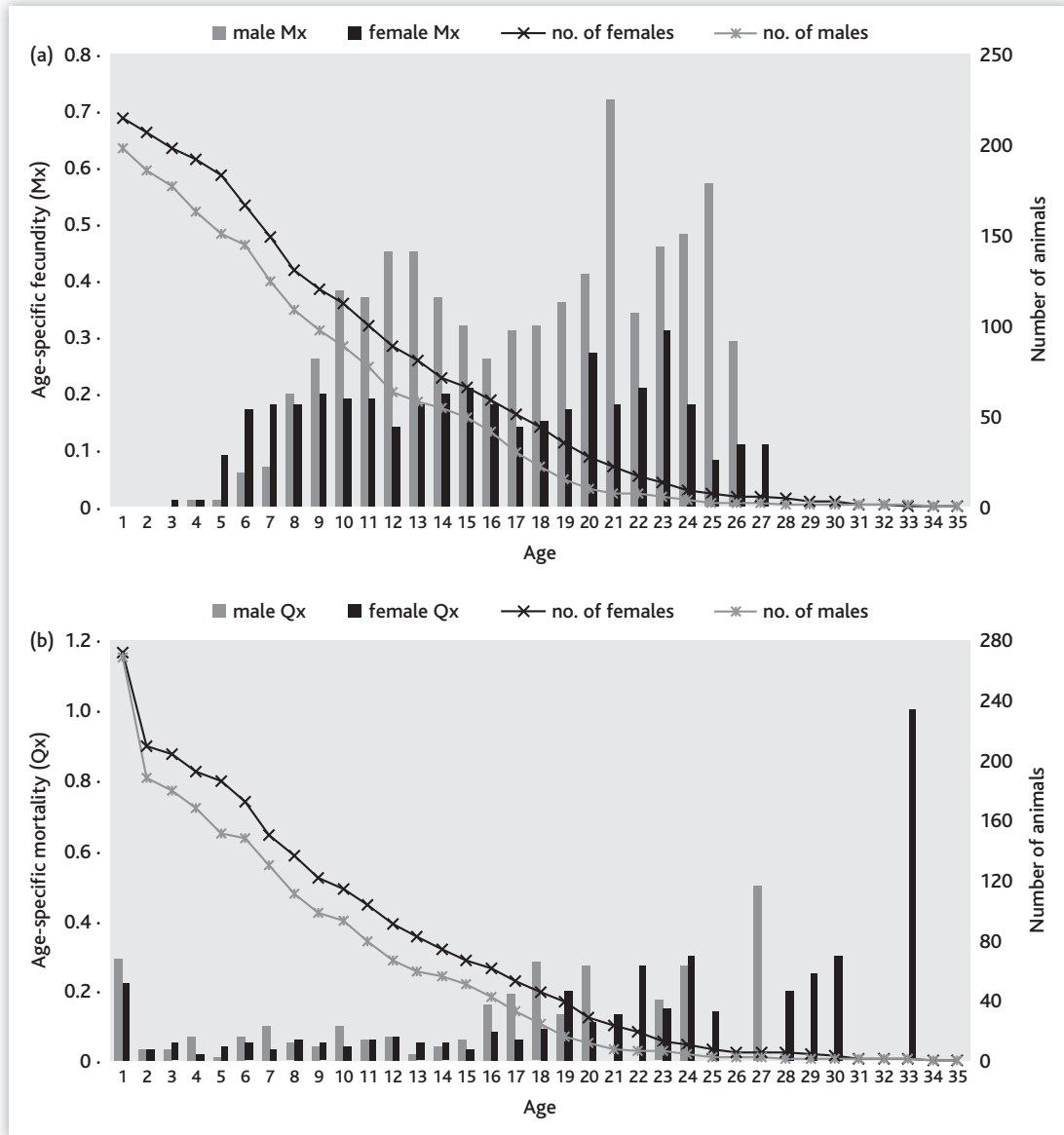
Figure 9.24 Analysis of data collated in the European Sulawesi macaque studbook since its inception provides information about fecundity (Mx) and mortality (Qx) levels that have occurred over time. For example, we can see from these graphs that (a) females start breeding before males and will continue breeding into their later twenties. We can also see from the data compiled for mortality rates (b) that there is a peak of deaths in the first year of life and then as animals get older. (Pictures: Vicky Melfi)

argues that, for some of these former species, such as butterflies, the need to maintain genetic diversity is only part of the conservation conundrum, because these species are highly sensitive to environmental change in the wild and this is reflected in genetic changes.

9.7.4 Common strategies employed in captive management

There are various strategies that can be adopted when managing captive animals. In some situations, the TAG or captive management

programme may make recommendations about which strategy should be adopted or considered most appropriate. In most circumstances, however, TAGs or regionally organized management programmes will make recommendations to a zoo that specific animals should or should not breed, but will leave the decision as to which strategy should be adopted to achieve these recommendations up to the zoo. The strategy adopted will be determined not only by species characteristics (for example, life history traits, reproductive biology, etc.), but also by the legal and ethical framework under which the zoo operates. It is important that a management strategy is identified and adopted, so that its efficacy can be monitored and, if it does not achieve its objectives, an alternative strategy can be sought.

So what strategies are there and how do we determine the most appropriate for a given species? Strategies can be categorized as those that aim to:

- increase the size of the captive population—for example, by providing animals with the opportunities to breed, or by facilitating successful breeding through artificial reproductive technologies;

- maintain or reduce the size of the captive population, which can be achieved by maintaining single-sex groups, by otherwise limiting access between differently sexed animals, by using contraception, or by operating 'breed and cull' strategies.

There are various considerations to bear in mind when choosing the most appropriate captive management strategy and these are summarized in **Table 9.5**.

	Health	**Behaviour**	**Legislation**	**Ethics**
Allowing breeding	Care needs to be taken that births do not start too early and that inter-birth intervals are not artificially shortened	–	–	Could potentially result in too many animals for which there is no space
Single-sex groups	–	Potential for aggression, lack of social interactions, and reduced opportunities for expression of natural behavioural repertoire	–	Might be considered 'unnatural'
Contraception	Potential detrimental side effects Animals may not be able to breed afterwards (even if contraception is considered temporary)	Potential detrimental side effects	Use is regulated by drug licensing, which means that not all formulations are easy to obtain	Pro-life lobby are against this
Breed and cull	–	–	Euthanasia may be restricted by law, e.g. it is illegal in some states of Germany	Pro-life lobby are against this

Table 9.5 An outline of the considerations affecting different captive management strategies

Note: No single captive management strategy is ideal, although the limitations inherent in the different strategies vary from potential health infringements to controversy over the ethical justification for some methods.

Some of the issues relating to the captive management of zoo animals—in particular, whether or not they should breed and which strategy is adopted to achieve this—attract more attention from people outside the zoo profession than most other areas of zoo animal housing and husbandry. This is partly because baby animals are perceived as 'cute' and therefore attract a lot of positive attention, but also because the methods used to prevent babies, or control against surplus animals (see **Box 9.8**), are viewed negatively. People's perceptions of using euthanasia as a management tool vary considerably for different species and in different regions (and euthanasia of zoo animals is not legal in some countries).

Box 9.8   SURPLUS ANIMALS

Animals can be labelled as surplus because of a lack of space, and this can be exacerbated by low rates of mortality and unrestricted breeding. Lack of space may occur because priority is given to another animal that is considered to be more important to the captive management of the species. By virtue of considering the types of animal that would benefit from a captive management programme, we can also identify which animals may be considered surplus if space is limited.

Animals that will be prioritized for inclusion in a captive management programme are those that are not related to other animals in the population (that is, they have a low mean kinship), of the right sex and age to create a demographically stable population, which is represented by a balanced sex–age pyramid, reproductively active, fit and healthy, and behaviourally competent.

Potentially, surplus animals could be avoided through better management programmes or they can be euthanized (reviewed by Glatston 1998). It seems an intuitive and simple idea to calculate the number of births required for a year and then to take measures, such as single-sex groups and contraception (see **section 9.6.2**), to ensure that only that number of offspring are born, so as to avoid a surplus. But this is overly simplistic, not only because 'accidents' happen, but also because the offspring born may not be suitable. For example, a surplus of male animals is often a problem with many species that are managed in harem systems, with one male maintained with several females, because many more females are required in the captive population than males.

Restricting breeding would limit the number of groups with young animals in them, and consequently deprive them of the positive social implications associated with young and reproductively active animals.

Alternatively, surplus animals can be culled, or euthanized, which is usually practised as part of a breed-and-cull programme. This term is used to describe situations in which animals are allowed to breed, but some animals from the group will be selected and culled to ensure that the group size remains constant. The selection of animals that will be culled can be variable, and is dependent, to some extent, on the group and their life history traits. For example, it may be appropriate that offspring are culled at the time that they would naturally leave their parents or emigrate from the group. Alternatively, older animals, which may represent post-reproductive or genetically well-represented individuals, or those less able to cope with **environmental challenges**, may be favoured as those chosen to be culled; animals falling in the latter category may have been culled for welfare reasons (see **section 7.3.3**). This method enables animals to express their full repertoire of reproductive behaviours, and ensures that fit and healthy animals are selected to contribute to the captive management programme, much akin to natural selection. But public perception and media coverage of euthanasia as a management tool, whether for welfare or conservation goals, is negative and unfortunately puts pressure on zoos to avoid using this measure, despite its many associated benefits for animals (see **Table 9.5**).
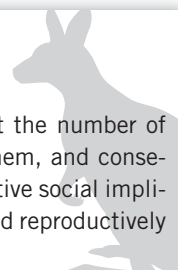
There also seems to be a popular assumption that, if zoo animals are not breeding, it is because the zoo is managing them incorrectly (and therefore their welfare is compromised) or the animals are not contributing to the conservation of species. For a long time, zoos promoted their role and their approach to conservation as one of species preservation (Tudge 1992). The analogy of zoos representing an ark (see **section 10.3**), which could conserve animals by keeping them safe in *ex situ* populations, propagating them, and then, when conditions in their native habitats were appropriate, releasing them into the wild, was popularized by many zoo professionals (Durrell 1976; Mathews *et al*. 2005). But this approach was recognized by Conway (1996b) and others to be rather too simplistic and to have inherent restrictions—that, in fact, conservation efforts would need to be much broader if zoos were proactively and effectively to conserve biodiversity (e.g. Hutchins and Wiese 1991) (see **Chapter 10**).

Unfortunately, there are many species held in zoos for which breeding, and life, in captivity is not coordinated and monitored by a regional management programme. In these situations, there is not necessarily a recommendation about whether or not breeding should take place, and so it is even more difficult to know which captive management strategy should be adopted. This can lead to the scenario in which a zoo may consider that they are 'just letting their animals live naturally' and consequently may, or may not, have offspring that, in time, will need to be re-homed. It is these situations—or, indeed, where preventative measures have failed—that create an issue of surplus animals.

Summary

- There is still a great deal to learn about exotic animal reproductive biology, because data collected thus far provide only a basic understanding of the complexities underpinning the various stages required to make a new life. As with all topics related to zoo animal management, the diversity of species managed in zoos compounds our lack of knowledge.

- Despite many of these gaps in our understanding, many zoos have been able to breed animals successfully using modifications to methodologies developed for animals in other industries; for example, efforts taken to create a self-sustaining population of captive elephants have involved the collection and analysis of data about the endocrinology and behaviour of elephants, the implementation of various assisted reproductive technologies, and, in some circumstances, supplementary rearing (see **Box 9.9**). But all of these efforts have greatly increased our knowledge of elephant reproduction and enhanced the welfare and management of captive elephant populations (Stevenson and Walter 2006).

- Similar work has also increased our ability to manage the captive populations of a great many other species, although there is yet much to learn and to apply to the successful breeding of other endangered species managed in zoos, which are hoped to represent a safety net and prevent the extinction of the species, even if they are lost in the wild habitat.

Further reading

Unlike some chapters in this book, in relation to which there is very little published information available beyond that cited in the text, the study of reproduction, genetics, and captive breeding of animals has resulted in a wealth of publications: academic, professional, and popular. Therefore to ensure that this section does not represent too long

Box 9.9 THE CAPTIVE MANAGEMENT OF ELEPHANTS

Zoo-housed elephants have been the focus of much attention in relation to their welfare and conservation (e.g. Clubb and Mason 2002; Hutchins 2006). In terms of the conservation of elephants in zoos, neither of the captive breeding programmes for African *Loxodonta africana* and Asian *Elephas maximus* species are currently self-sustaining. In fact, analyses of data collected from the Asian elephant captive management programmes has shown that the population is declining at a rate of 2 per cent per annum (Faust *et al*. 2006).

To reverse this trend and to work towards self-sustaining captive elephant populations, more offspring are needed. A variety of techniques are currently being explored and implemented to investigate why zoo populations of elephants are not breeding successfully and also to facilitate breeding. Studies of the elephant's endocrine function have also been conducted to evaluate different reproductive stages in females (for example, predictors of ovulation and parturition) and males (for example, maturation and musth) (Cooper *et al*. 1990; Brown and Wemmer 1995). Hormone profiles and **ultrasound** results found that a number of captive elephants were not cycling in 14 per cent of 49 respondent zoos that held Asian elephants and 29 per cent of 62 respondent zoos that held African elephants (Brown *et al*. 2004).

To complicate elephant reproduction further, social factors that affect the ovarian cycle have also been identified, including dominance rank (Freeman *et al*. 2004).

On a positive note, however, initial examinations of female reproductive tracts used to develop AI techniques have proved successful, resulting in some AI babies (Balke *et al*. 1988) (**Fig. 9.25**).

(a)

(b) 0–1Afr'eleph–Tanja   Colchester Zoo

GBH

C60

9
22
2001Jul01   15:10

Original ultrasound image
of Tanya's baby
(early embryo)

Ultrasonographic
3D-reconstruction
of an embryo
of this stage

ZOO COLCHESTER
and ProGenY

2001

Magnification of the image
sector where the embryo
is situated
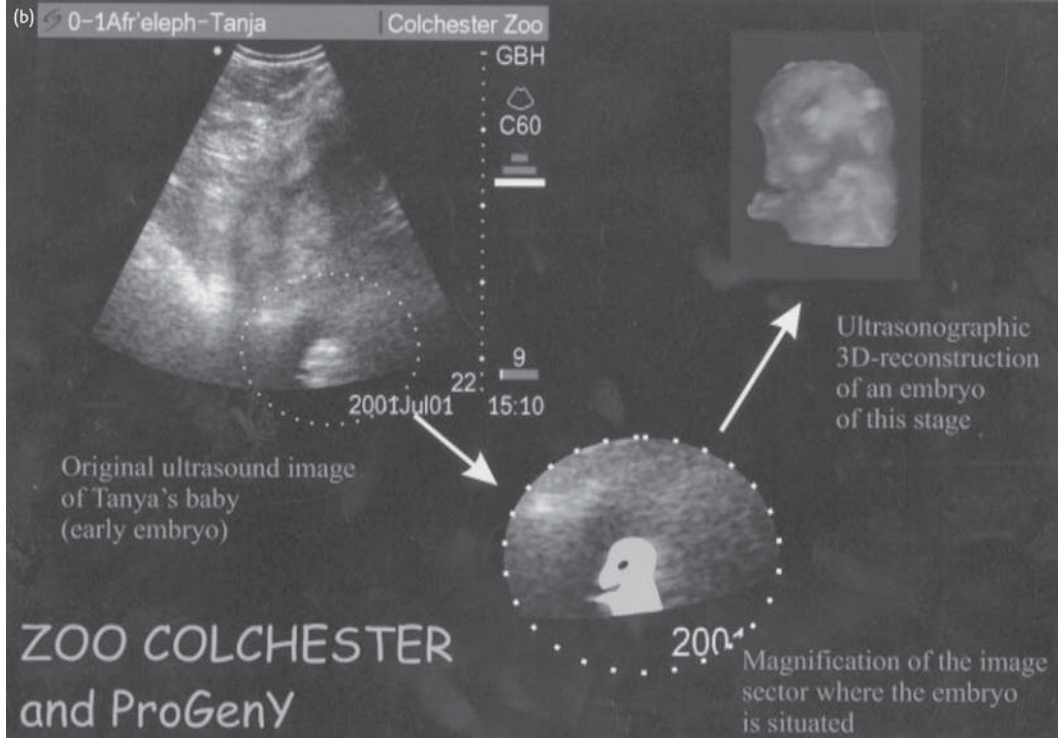
Figure 9.25 Elephant populations in zoos are still not self-sustaining, but efforts are being taken to reverse this trend through the use of (a) artificial insemination and (b) proactive monitoring of reproductive state, using techniques such as ultrasonography (which is able to follow the development of the fetus). If all goes well, this work is repaid with a successful birth, as (c) pictured here at Colchester Zoo. (Photographs: Colchester Zoo)

a list, we have highlighted only a couple of key texts for each of the main topics considered in this chapter, and we have tried, where possible, to refer to texts that have exotic animals and zoos as their central focus.

Genetics and captive population management

Frankham *et al.*'s *Introduction to Conservation Genetics* (2002) provides all the necessary theory on the basis of which decisions are made about how to manage a captive population, with respect to its genetic integrity. If this is a little too heavyweight, try Frankham *et al.*'s *A Primer of Conservation Genetics* (2004).

Reproduction and contraception

Holt *et al.*'s *Reproductive Science and Integrated Conservation* (2003) provides a very comprehensive overview of exotic animal reproduction, while Asa and Porton's *Wildlife Contraception: Issues, Methods and Applications* (2005) considers the methods, and their implications, used to prevent offspring in exotic species. Wishart (2001) provides a useful review of sperm cryopreservation and AI in birds. A collaborative workshop between the Chinese Association of Zoological Gardens (CAZG) and the IUCN's Conservation Breeding Specialist Group (CBSG) on captive breeding of the giant panda *Ailuropoda melanoleuca* resulted in the development of better methodology for the cooling and cryopreservation of panda sperm (reported in Wildt *et al.* 2003).

Captive breeding in zoos

Colin Tudge's *Last Animals at the Zoo: How Mass Extinction can be Stopped* (1992) has done a great deal to popularize the concepts behind captive breeding programmes. Quite a few different journals have also had special issues dedicated to the subject of captive breeding—for example, the *International Zoo Yearbook* and *Conservation Biology*.

General texts

Kleiman *et al.*'s *Wild Mammals in Captivity* (1996; 2010) provides a very thorough review of many of the topics covered in this chapter, obviously for the mammalian taxa. Norton *et al.*'s *Ethics on the Ark* (1995) explores many of the controversial issues raised by the captive management of animals in zoos.

Websites and other resources

It is probably prudent to consider the above texts as the best port of call for further detail about the theory underpinning many of the issues discussed in this chapter, whereas the websites available can provide more information about how animal management programmes operate in practice.

The various zoo association (AZA, EAZA, etc.) websites provide much detail about the captive management programmes that they run, along with varying degrees of additional information. The AZA Wildlife Contraception Center (WCC), a contraceptive advisory group to the AZA, has a very good website (**http://www.stlzoo.org/animals/scienceresearch/contraceptioncenter**) featuring recommendations and lots more.

In Europe, a new EU zoo contraception advisory group is under development, referred to as the European Group on Zoo Animal Contraception (EGZAC). The aim of EGZAC is to collect information from European zoos on contraception recommendations and product availability within the EU, and, over the longer term, to merge this information with the AZA's WCC database.

The website of the Frozen Ark Project (**http://www.frozenark.org**) has already been mentioned in this chapter; this site has very good short explanations of topics such as 'Why DNA?' and the viability of frozen cells and tissue.

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.
http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Chapter 10
Conservation

Conservation of endangered species is now one of the major goals of accredited **zoos**.

The emphasis on a conservation role for zoos grew greatly in importance during the 1970s and 1980s, prompted partly by the zoos themselves and partly by external pressures, such as new international treaties and national legislation. To members of the public, the focus on conservation is probably most apparent in the signs and labels at the zoo, which draw attention to breeding successes, particularly of rare species, and also in zoo websites and literature, which prominently feature zoos' conservation priorities and activities. The increasing importance to zoos of an active involvement in conservation has been accompanied by a reduction in the number of different species maintained, more coordinated cooperation between zoos, and a great reduction in the number of animals taken from the wild. In recent years zoos have also expanded their involvement in field conservation projects, supporting and engaging with conservation of animals outside the zoo, in their natural habitats. This has occurred alongside increasing criticism not only of what zoos could do, but also of what they were actually doing to conserve rare species. In the last few years, in the light of what appear to be increased threats to natural habitats, including those due to climate change, the potential role of zoos in conservation has become more prominent once again. In this chapter, we will consider the following.

Boxes in this chapter provide additional information on special topics and case studies, such as EAZA conservation campaigns and efforts to conserve endangered *Partula* snails.

10.1 What is 'conservation' and why is it necessary?

The term 'conservation' is used in a number of different ways and contexts, and can, for example, refer to the restoration of artistic artefacts in museums, or to saving a historic building from demolition. In the context of species and environments, a typical definition of a conservationist is '*someone who advocates or practises the sensible and careful use of natural resources*' (Hunter 1995). Implicit in this definition is the idea of

human intervention and management to achieve some kind of sustainable usage of resources.

Some conservationists make a distinction between conservation and 'preservation', in which management would be minimal and resources would be kept as pristine as possible. Indeed, 'preservationist' is seen by many conservationists as a rather negative term. Despite these niceties, however, preservation is effectively what conservationists do, although in an active and interventionist way.

Mace *et al.* (2007) offer a simpler definition of conservation as '*the persistence of wild habitats and species*'. This is a useful definition to bear in mind when we talk about measuring the success (or otherwise) of conservation initiatives by zoos and, indeed, is broadly similar to the definition of conservation that zoos themselves have proposed in the World Zoo and Aquarium Conservation Strategy (WZACS) (WAZA 2005) (see **section 10.2.2**). WZACS defines conservation as '*the securing of long-term populations of species in natural ecosystems and habitats wherever possible*'.

The science that underpins conservation is conservation biology, which, as the term would suggest, is heavily based on biology, but draws on other disciplines as well. It may be defined as '*the applied science of maintaining the earth's biological diversity*' (Hunter 1995).

10.1.1 Biodiversity

Today, the terms 'conservation' and biodiversity[1] are often used together, to make explicit the distinction between the conservation of living organisms and non-living structures, such as buildings or books. Another way of defining biodiversity would be as '*the totality of genes, species and ecosystems in a region*' (WRI/MCN/UNEP/FAO/UNESCO 1992).

So biodiversity is concerned with the variety and variability of different kinds of animals and plants, the genes that make them what they are and give them their adaptability (for example, to changing environments, to evolving diseases, etc.), and the associations and communities in which they live.

For the remainder of this chapter, when the word 'conservation' is used, this will mean the conservation of biodiversity, not just of animal biodiversity, but also plants and ecosystems, which are also the concern of zoos.

10.1.2 Why is conservation necessary?

Conservation biology, as defined in the previous section, is concerned with trying to maintain biodiversity. As we are all now very aware, biodiversity is under threat as a result of human impact on the environment (Wilson 1988; Reaka-Kudka *et al.* 1996).[2] Human pressure on the places in which animals live (for building, agriculture, tourism, and sometimes simply wanton destruction) is causing an unprecedented loss of habitats. Habitat destruction and hunting have already resulted in the extinction of many species, and many more will follow in the next couple of decades. It is not only terrestrial habitats that are under threat; pollution and drainage schemes threaten lakes and rivers, and over-exploitation and pollution threaten marine species (Jenkins 2003). The introduction of invasive non-native or exotic species, whether deliberate or accidental, is another major contributor to the extinction of species, particularly of endemics. Climate change (global warming) presents an additional threat to terrestrial and marine habitats alike, with a prediction by Thomas *et al.* (2004) that

---

[1] Biodiversity' is shorthand for biological diversity. The term was first used by US scientist Walter Rosen as the title for a National Forum held in Washington, DC, in 1986. Papers from this forum were subsequently published in an influential book, edited by E. O. Wilson, with the title *BioDiversity* (1988).

[2] Reaka-Kudka *et al.*'s *BioDiversity II: Understanding and Protecting our Natural Resources* was published in 1996 as a follow-up to Wilson (1988).

mid-range warming to 2050 could result in the loss of between 15 and 37 per cent of animal and plant species.

William Conway (former president of the World Conservation Society and director of the Bronx Zoo) has said that '*we live in an age of extinction*' (Conway 2007). But just what is the scale of this extinction? Extinction is, of course, a natural part of the evolutionary process and it is often said that most of the species that have ever existed are now extinct. In the context of the current extinction crisis, we should treat such a statement with some caution. Firstly, many of those species in geological time have not become extinct as such; they have evolved into different species.

Secondly, it is clear that the rate of species extinctions that we are now experiencing is very much greater than that which has happened throughout evolutionary time. An estimate of pre-human extinction rates (that is, a 'natural' rate) gives a figure of about three species per year for described species—twenty-five per year if we accept that most species are unknown to science (Magin *et al.* 1994). Since 1600 (when records first become available), over 490 species of animals (mostly molluscs, mammals, and birds) are known to have become extinct; if corrections are made for invertebrates (which are generally not in the historical records), then an estimated 18,000 of described species and 140,000 of all species (including those not yet known to science) have become extinct since 1600 (Magin *et al.* 1994). Even if only birds and mammals are considered, the expected losses to extinction in the period since 1600 would be four species of mammals and nine of birds; the actual known extinctions (up to the publication of Magin *et al*'s paper) are sixty mammals and 122 birds.

A more recent listing (Baillie *et al.* 2004) identifies 784 species (338 vertebrates; 359 invertebrates; eighty-six plants; one protist[3]) have become extinct in recent history, and a further sixty (twenty-two vertebrates; fourteen invertebrates; twenty-four plants) that have become extinct in the wild, although they still exist in captivity. There is some evidence that even this rate of extinction is increasing. At least nine, and possibly as many as 122, species of amphibians have become extinct since 1980, including possibly thirty of the 113 known species of harlequin toads (genus *Atelopus*) alone (Mendelson III *et al.* 2006). Amongst birds and mammals, between 1988 and 2008 on average fifty-two species per year moved one IUCN Red List[4] category closer to extinction, and two bird species became extinct (the Hawaiian kamao *Myadestes myadestinus* and the Alaotra grebe *Tachybaptus rufolavatus*), with a further six possibly extinct (Hoffman *et al.* 2010). And just in the last ten years, at least one species of large charismatic mammal (the Yangtze river dolphin *Lipotes vexillifer*) has become extinct (Turvey *et al.* 2007), and several large mammalian subspecies, such as the Chinese white-handed gibbon *Hylobates lar yunnanensis* (Melfi 2012a) and possibly the Northern white rhinoceros *Ceratotherium simum cottoni* (Carwardine 2009), have become extinct in the wild.

The extinct list includes some well-known species, such as the dodo *Raphus cucullatus* (last reported in 1662) (**Fig. 10.1a**), the great auk *Pinguinus impennis* (last seen alive in 1852), the quagga *Equus quagga quagga* (the last known animal died in Amsterdam Zoo in 1883) (**Fig. 10.1b**), the passenger pigeon *Ectopistes migratorius* (the last known animal died in Cincinnati Zoo in 1914) (see **Box 2.2**), and the thylacine *Thylacinus*

---

[3] Protists are mostly unicellular organisms, although some are multicellular. Some protists (e.g. protozoans) are animal-like, whereas others (algae) are plant-like. These are organisms that do not fit neatly into categories such as animal, plant, or fungus.

[4] The full name of the Red List is the IUCN Red List of Threatened Species. This can be viewed online on the IUCN website. At the time of writing, the latest Red List is the list of 2012, which was released at the Rio +20 Earth Summit.

Figure 10.1 Two well-known species that became extinct within historic times. (a) The dodo *Raphus cucullatus*, which was probably the first extinction for which we have documented evidence; this skeleton (there are no stuffed specimens) is on show at the Durrell Wildlife Conservation Trust in Jersey, where the dodo is the Trust's symbol. (b) The quagga *Equus quagga quagga*; it is possible that this species survived in the wild until the late 1870s, but the last known specimen died in Amsterdam Zoo in 1883 and is now in the Zoological Museum in Amsterdam. Modern evidence suggests that the quagga belongs to the same species as Burchell's zebra, formerly called *Equus burchelli*, but probably now best referred to as *Equus quagga burchelli*. (Photographs: (a) Geoff Hosey; (b) F.York, London, Regent's Park, 1870)

Figure 10.2 The thylacine *Thylacinus cynocephalus*. This large predatory marsupial probably became extinct on the Australian mainland 2,000 years ago (possibly through human activity), but survived on the island of Tasmania until the early years of the twentieth century, when it was hunted to extinction. The last known specimen died in Hobart Zoo in 1936. (Photograph: courtesy of the Australian Museum)

cynocephalus (**Fig. 10.2**). It also includes many that are not widely known, such as forty-eight species of *Partula* snails (see **Box 10.1**) and thirty species of cichlids (a type of fish) of the genus *Haplochromis*.[5]

In the 20 years from 1984 to 2004, at least five species of animals (Wyoming toad *Bufo baxteri*, Hawaiian crow *Corvus hawaiiensis*, Alagoas curassow *Crax mitu*, Guam rail *Gallirallus owstoni*, and scimitar-horned oryx *Oryx dammah*) have

---

[5] Most of the now-extinct species of cichlids of the genus *Haplochromis* are restricted to Lake Victoria, where they have been decimated by the introduced predator the Nile perch *Lates niloticus*.

Box 10.1 SMALL IS BEAUTIFUL: SAVING THE *PARTULA* SNAILS

When talking about wildlife conservation, many people tend to think of large charismatic mammalian species like giant pandas, tigers, and elephants. But small species can be just as charismatic, and much effort has gone into saving some of the little animals that might so easily be overlooked.

A good example is the case of the *Partula* snails. These are small spiral-shelled land snails, usually less than 20 mm in length (**Fig. 10.3**). They live on the islands of French Polynesia in the Pacific Ocean, where they have evolved into over a hundred different species through the process of adaptive radiation, just as the more familiar Galapagos fauna has done.

But these little snails have been vulnerable to a number of threats. The chief of these is a predatory snail *Euglandina rosea*, which was introduced into Polynesia in the 1970s in an attempt to control another introduced species, the African giant land snail *Achatina fulica*, which had become an agricultural **pest**. Unfortunately, *Euglandina* found the *Partula* snails to be a perfectly acceptable meal and, because partulids reproduce rather slowly (because they give birth to live young), they declined in numbers. By the late 1980s, all partulid species were extinct on the island of Moorea (Murray *et al.* 1988). By the start of this century, fifty-six out of sixty-one species of *Partula* had become extinct throughout the Society Islands (which include Tahiti, Moorea, and others), primarily because of predation by *E.rosea* (Coote and Loeve 2003).

Fortunately, there have been **captive assurance programmes** (the Partula Conservation Programme), coordinated since 1994 by the Zoological Society of London (ZSL). This programme involves both captive breeding (for twenty-five species in fifteen different zoos worldwide) (**Fig. 10.4**) and fieldwork within the snails' natural habitat. A successful release of zoo-bred *Partula taeniata* into semi-free range (among Polynesian plants in the Palm House at the Royal Botanic Gardens at Kew) showed that they were capable of displaying the behaviours needed for life in the wild (Pearce-Kelly *et al.* 1995).

Since then, several have been released into enclosures back on Moorea, where all the species were previously thought to have become extinct (Coote *et al.* 2004). Unfortunately, *E.rosea* is still there and still partial to partulas, but enclosed areas may provide refuges for reintroduced partulas in the future. It also appears that some of the *Partula* species on Moorea had not become extinct after all (Lee *et al.* 2009), giving additional hope to efforts to save these species.

Figure 10.3 *Partula rosea*, along with many others snails in this genus, are critically endangered (as listed by the IUCN) in their native habitat of French Polynesia because of the introduction of a predatory snail, which unfortunately preferred to eat them rather than the pest African giant land snail that was its intended target. (Photograph: Doug Sherriff)

Figure 10.4 As you can see from the mating behaviour of these *Partula faba*, they are currently being managed as part of a very successful captive management programme, which is their last hope for survival because they are extinct in the wild. (Photograph: Doug Sherriff)

become extinct in the wild and now exist only in captivity (Baillie *et al.* 2004) (**Fig. 10.5**), and we can now add the Kihansi spray toad *Nectophrynoides asperginis* and the Socorro dove *Zenaida graysoni* to this list (Conde *et al.* 2011). These are just the ones we know about. The status of many small or obscure species, particularly invertebrates, has never been surveyed, and it is perfectly possible that some of them have slipped away without us even being aware of it.
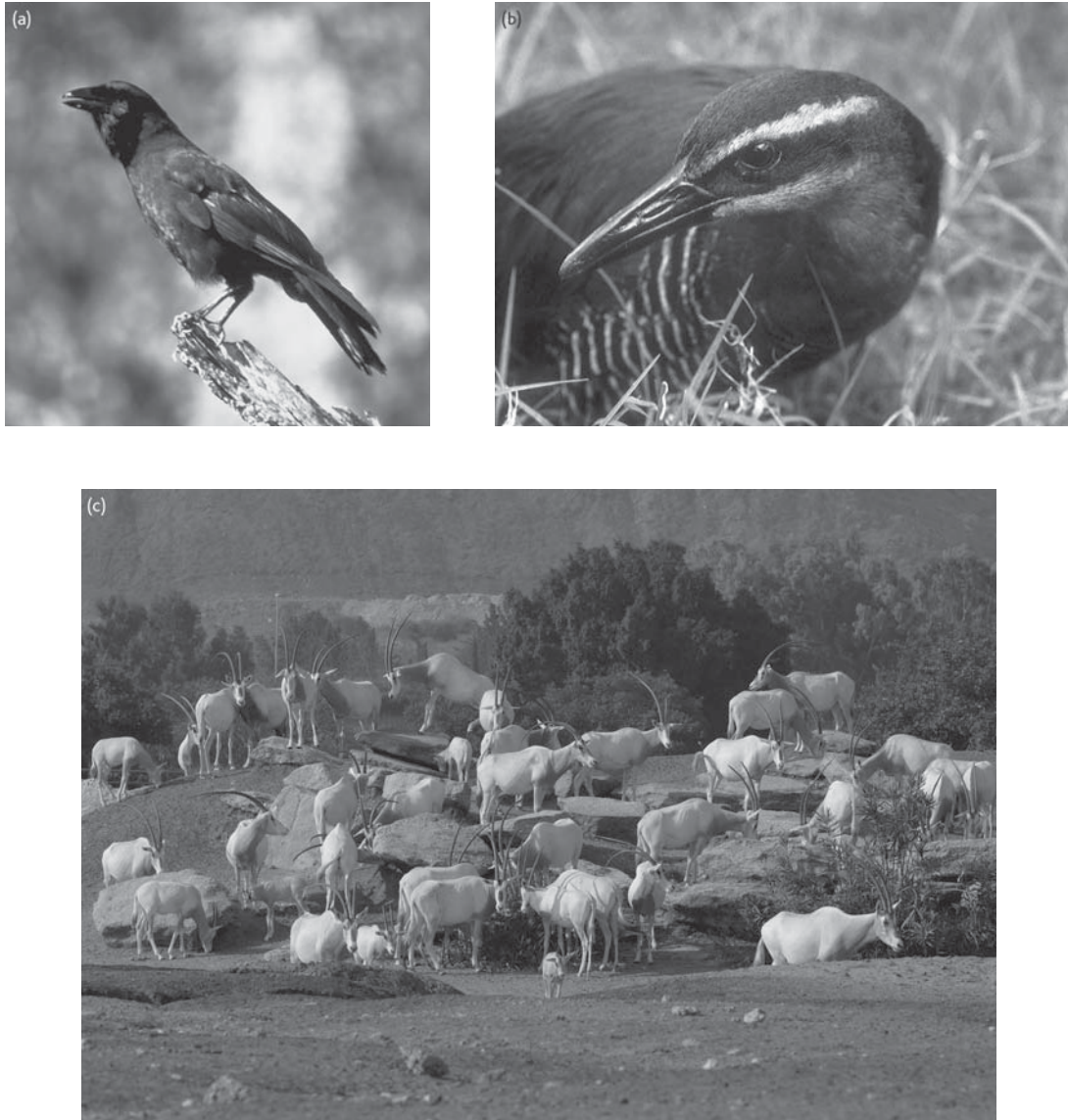
Figure 10.5 These three species represent animals that are extinct in the wild and the future survival of which depends on their successful captive breeding. Reintroduction of individuals back into their native habitats is being attempted for all three species: (a) the Hawaiian crow *Corvus hawaiiensis*, the last known wild specimens of which died in 2002; (b) the Guam rail *Gallirallus owstoni*, which disappeared in the wild during the 1980s as a result of predation by the introduced brown tree snake *Boiga irregularis*; (c) the scimitar-horned oryx *Oryx dammah*, which was probably exterminated by overhunting in the 1980s. (Photographs: (a) US Fish and Wildlife Service; (b) Smithsonian's National Zoo; (c) Tibor Jäger, Zoological Center Tel Aviv–Ramat Gan, Israel)

So, are human-generated extinctions increasing? In general, the answer is 'yes', and 20 years ago there were predictions that between 2 and 25 per cent of species would be lost by 2015 (Magin *et al.* 1994). In fact, it now looks likely that two-thirds of the world's species could be lost by the end of this century (Raven 2002). During the twentieth century, extinction rates were higher than the fossil evidence's background rates by a factor of 100–1000, and there is evidence that there will be a further tenfold speeding up of the rate over the coming century (May 2011).

Of the land mammals, disproportionately represented in zoos, Ceballos *et al.* (2005) suggest that approximately a quarter of all species are now at risk of extinction. Attention, then, must be on the species that still exist, but which are threatened with extinction. The 2007 IUCN (World Conservation Union) Red List of Threatened Species[6] gives a total of 5,742 vertebrate species and 1,601 insect (**Fig. 10.6**) and mollusc species at risk—that is, categorized by the IUCN as 'vulnerable', 'endangered', or 'critically endangered'. By 2012 these figures had gone up to 7,250 for vertebrates and 3,570 for invertebrates (IUCN 2012).

Of course, these are only the species where enough is known about their status in the wild for this designation to be made; while many of the known species of land vertebrates have been evaluated, very few invertebrates have been (fewer than 4,000 out of over a million named species). Indeed, a large number of species are categorized as 'data deficient', and the fact that we have no idea about their status probably means that they are also endangered. This, then, is an enormous list of species that need active conservation measures if they are to survive.

So the current and future scale of extinctions is enormous. Why does it matter? In general we

Figure 10.6 An example is shown here of an endangered insect, the Frégate Island giant beetle *Polposipus herculaneus.* This flightless beetle is endemic to one island in the Seychelles archipelago, where its numbers have been severely reduced through predation by introduced rats. It is now listed as critically endangered by IUCN, and its conservation includes both *in situ* (such as eradication of rats) and *ex situ* (captive breeding) initiatives. This photograph was taken at the Zoological Society of London; the spot on each beetle is an identification marker. (Photograph: Sheila Pankhurst)

have little idea of how the loss of biodiversity will affect the ordinary way we live our lives; additionally, we are only now starting to realize the potential value of different species not only to our ecosystems, but also to tourism, medicine, agriculture, and so on; and finally there are strong ethical reasons for believing that it is right to try to conserve biodiversity (May 2011).

In this chapter, we are concerned with looking at what role zoos can play in this conservation effort.

---

[6] The IUCN Species Survival Commission (SSC) maintains the Red List database, from which the Red List of Threatened Species is produced. This list is updated at least every two years. The IUCN/SCC Red List should not be confused with the many Red Data Books in circulation. The latter are national or regional accounts of endangered species, and usually deal with a specific group of animals or plants (for example, the Red Data Book of European Butterflies).

10.2 The role of zoos in the conservation of biodiversity

Zoos can play an active role in conservation in four general areas.

• Maintenance of captive stocks (see **Chapter 9**) of endangered species (and **reintroduction** of these animals back into the wild where possible). This is the idea that zoos can act as a kind of 'ark', a place where populations of endangered species can be maintained in safety until such time as they can be put back into the wild. This role will be considered in more detail below.

• Support for, and practical involvement with, *in situ* **conservation** projects. Many would argue that the most efficient and effective way to ensure species survival is through conservation efforts within the wild home ranges of those species. Zoos could contribute to this with, amongst other things, animal planning expertise, infrastructure, and financial support. This aspect of zoo conservation activity will also be considered in more detail below.

• Education and campaigning about conservation issues. There are many reasons why people visit zoos, but once in the zoo they represent a 'captive audience', which zoos can use to raise awareness and knowledge of conservation issues. This can be achieved through enclosure design, signage, keeper talks, interactive education, animal shows, and in other ways. Indeed, it is as important sometimes to keep species of low conservation importance in zoos[7] as it is to keep the high-priority species, because they may be more useful in promoting the conservation message by enhancing people's zoo experience of animals. Endangered species provide a direct message about conservation, but related non-endangered species can act as an analogy for these, and give additional messages when used elsewhere in the zoo. Successful education must be targeted appropriately and must take due account of what are sometimes perceived by the public as the more negative aspects of zoos (Whitehead 1995). For example, large charismatic species such as elephants have the potential to be used in effective education, but this effectiveness has not yet been demonstrated (Clubb and Mason 2002). The effectiveness of zoo education initiatives remains unclear and it is likely that the most important educational aspect of zoo conservation is simply the caring values shown by zoos in their dealings with animals (Rabb and Saunders 2005). More is said about this aspect of zoo work in **section 13.2.3.**, so it will not be considered any further here.

• Research that benefits the science and practice of conservation. For many years, research (see **Chapter 14**) conducted on zoo animals tended to be concerned primarily with anatomy and taxonomy, but there is a huge potential in zoos to undertake behavioural, genetic, and physiological research that contributes to the *in situ* and *ex situ* **conservation** of endangered species (Ryder and Feistner 1995). The importance of research is even more prominent in WZACS, which, among other things, urges zoos to formulate proper research plans within their resources, to promote and carry out research, to contribute to databases, and to disseminate their research findings. How well zoos do this is not altogether clear. Rees (2005b), for example, maintains that most of the research studies done in zoos are not directly relevant to conservation (for example, behavioural studies and studies on **environmental enrichment**). While it is the case that behavioural studies predominate in zoo research in the UK (in the US, physiology predominates), there is also

---

[7] A good example of a species of low conservation importance that is often a very popular zoo exhibit is the meerkat *Suricata suricatta.* These animals are not considered to be endangered in their native habitat in southern Africa, but meerkats are highly social, and are regarded as an attractive and engaging species that appears to have few welfare problems in captivity.

substantial interdisciplinary research on captive breeding (see **section 14.3.3**). In any case, it is becoming increasingly clear that behavioural studies are of importance to conservation (Shepherdson 1994; Wielebnowski 1998; Festa-Bianchet and Apollonio 2003; Swaisgood 2007; Becker *et al.* 2012), not least because of the need to maintain **behavioural diversity** and survival skills in captive animals that may become candidates for reintroduction.

These conservation roles and activities have been defined in three strategy documents: the *World Zoo Conservation Strategy* (IUDZG/CBSG 1993) and its successor, the *World Zoo and Aquarium Conservation Strategy* (WAZA 2005) (**Fig. 10.7**), and *Turning the Tide* (WAZA 2009), which looks specifically at what the aquarium community can do to support conservation. These documents are considered in more detail in **section 10.2.2**, but let us first look more closely at the concepts of *in situ* and *ex situ* conservation.

10.2.1 *Ex situ* versus *in situ* conservation

The best place to maintain biodiversity is, of course, in the natural habitats in which animal and plant species live, and this is known as *in situ* conservation. However, it is now apparent to most people that, for various reasons, *in situ* conservation is not a reliable or safe option for some of the most endangered species and that, if they are to be conserved at all, this can only be done away from their natural habitat, in zoos and wildlife parks. This is *ex situ* conservation.[8] The expectation of modern zoos is that they will be involved in both
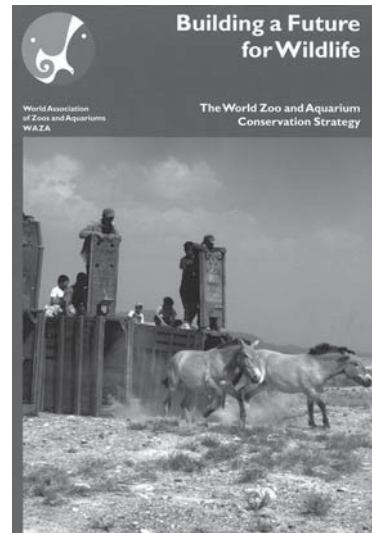
Figure 10.7 The World Zoo and Aquarium Conservation Strategy (WZACS), WAZA's framework for the role of zoos in conservation. The cover shows female Przewalski's horses *Equus ferus przewalskii*, being released into the Gobi B National Park in Mongolia. Also known as the Mongolian wild horse, this species became extinct in the wild during the 1960s. (Photograph: WAZA)

ex situ and *in situ* conservation, as part of an integrated strategy.

The terms '*ex situ*' and '*in situ*', in relation to the conservation of biodiversity, are set out in the text of the Convention on Biodiversity (CBD) (UN 1992), the international conservation treaty that resulted from the Rio Earth Summit[9] in 1992.

The CBD made some very specific recommendations on *ex situ* conservation and these recommendations have been a major driving force pushing conservation to the forefront of the zoo agenda. The Rio Earth Summit and the CBD have already been discussed in **Chapter 3** (in the context of the regulatory framework for zoos), but it

[8] There is some debate within the zoo community about the practical use of the terms *in situ* and *ex situ*. Animals kept in sanctuaries in their country of origin, for example, may not be considered *in situ* if the sanctuary is fenced and if the animals are not free to migrate out of the immediate area.

[9] The so-called Rio Earth Summit is more properly referred to as the United Nations Conference on Environment and Development (UNCED), which took place in Rio de Janeiro, Brazil, in June 1992. Apart from the Convention on Biodiversity (CBD), another output of the 1992 Rio Earth Summit was the United Nations Framework Convention on Climate Change (UNFCCC). The better known Kyoto Protocol is an addition to the UNFCCC.

is worth stating again here that Article 9 of this treaty sets out that:

'Each Contracting Party shall, as far as possible and as appropriate, and predominantly for the purpose of complementing in situ measures:
(a) Adopt measure for the ex-situ conservation of components of biological diversity, preferably in the country of origin of such components
(b) Establish and maintain facilities for ex-situ conservation of and research on plants, animals and micro-organisms, preferably in the country of origin of genetic resources'

Article 9 of the CBD also lists other measures relating to *ex situ* conservation. These are set out in full in the WZACS (WAZA 2005), which is discussed in **section 10.2.2**.

10.2.2 Frameworks for zoo conservation

There are a myriad of strategies and prioritization proposals. WAZA has a large global membership, so its publication WZACS, which sees an integrated approach through both *in situ* and *ex situ* conservation, has the greatest support. Further elaboration of this integrated approach comes in *Catalysts for Conservation* (Zimmermann *et al.* 2007), which envisages zoos becoming 'conservation centres'. For the aquarium community, a key document is *Turning the Tide*, which considers the implementation of WZACS for WAZA aquariums. Let us look more closely at these documents.

The World Zoo and Aquarium Conservation Strategy (WZACS)

The current *World Zoo and Aquarium Conservation Strategy* (WZACS) was published in 2005 under the title *Building a Future for Wildlife* (WAZA 2005). WZACS builds on the earlier *World Zoo Conservation Strategy* (WZCS) (IUDZG/BSG 1993), which was a joint venture of the World Zoo Organization (now WAZA) and the Captive Breeding Specialist Group (CBSG) of the IUCN's Species Survival Commission (SSC).[10]

Although WZCS has now been superseded by WZACS, it is worth looking at how this first zoo conservation strategy document came about and what its goals were. WZCS aimed to identify how zoos could be involved in conservation, and also how they could formulate policies and procedures to achieve conservation goals. Another aim of the document was to raise awareness of, and support for, the conservation efforts of zoos among other agencies and authorities.

WZCS suggested that zoos should support the objectives of the *World Conservation Strategy*[11] by conserving populations of endangered species both *in situ* and *ex situ* through coordinated programmes, by undertaking conservation-related research and providing facilities for others to do the same, and by promoting greater public and political awareness of the importance of conservation. Although these were activities in which many zoos were already involved, by incorporating them into a written document, WZCS effectively formulated a set of standards against which the conservation activities of zoos could be judged (Waugh 1988; Wemmer *et al.* 1993; Wheater 1995).

From WZCS to WZACS

Much of WZCS was informative, outlining the theory and practice of conservation as undertaken by zoos. WZACS, its successor, is not really a new version of the strategy, but rather a further elaboration of the policies and standards that should be reached in achieving the conservation goals of the strategy. Thus, in each of the areas in which zoos have a role to play, WZACS provides a stated vision, supporting information, and a set of recommendations towards which zoos are to work.

An important aspect of WZACS is its advocacy of **integrated conservation**, which involves the

[10] For those readers who are reeling from acronym overload and having trouble separating their 'WZCS' from their 'WZACS', take a moment to re-read the **List of acronyms** at the front of this book.

[11] The *World Conservation Strategy* was published by the IUCN in 1980 and essentially advocates ecologically sound development in the world's nations.

bringing together of different activities and different agencies in order to achieve conservation priorities (see **section 10.4.1**). An interpretation of WZACS is provided in WAZA (2006).

Catalysts for conservation

At the same time as the regulatory framework for zoos has changed to include explicit commitments to *ex situ* conservation, zoos are also being expected to expand their involvement in, and support for, *in situ* work. A symposium on the role of zoos as catalysts for *in situ* conservation was held in London in 2004, co-hosted by the Zoological Society of London (ZSL) and the New York based Wildlife Conservation Society (WCS).

One of the outcomes of this meeting (Zimmerman *et al.* 2007) was the creation of a list of specific conservation-related challenges for zoos, including: '*All activities of zoos and aquaria should be conceived and designed to contribute to achieving the overall goal of in situ conservation.*' In other words, zoos should undertake *ex situ* work only as part of an integrated strategy, ultimately directed towards the conservation of species in their natural habitats. (The concept of integrated conservation and how to make this work in practice is discussed in more detail in **section 10.4.1**.)

Turning the Tide

In 2009, WAZA published a new strategy document, *Turning the Tide: A Global Aquarium Strategy for Conservation and Sustainability* (WAZA 2009). This opens with the following quotation from Rachel Carson (author of the highly influential book, *Silent Spring*):

'There has long been a belief that the sea, at least, was inviolate, beyond man's ability to change and to despoil. But this belief, unfortunately, has proved to be naïve'

Rachel Carson, *The Sea Around Us*, 1951

The stated aim of *Turning the Tide* is to chart a course for the implementation of WZACS by the world aquarium community against the backdrop of increasing concern about loss of biodiversity in aquatic ecosystems worldwide. As with WZACS, the strategy provides a series of specific recommendations and actions, addressing issues such as fund-raising for *in situ* conservation, and the need to focus conservation activities within existing frameworks set by local, national, and regional species survival plans and biodiversity action plans (WAZA 2009).

10.3 Zoos as arks

Defining the conservation role of zoos in both theory and practice is, as we have just seen, an ongoing process. Just 20 or so years ago, many people would probably have seen the maintenance of zoo populations of endangered species as being the major component of this role. From this perspective, zoos are seen as modern arks, keeping species safe from extinction until a time at which it is possible to re-establish them safely in the wild. This activity is still seen as important, although it is only one of a number of important conservation activities in which zoos should be engaged.

10.3.1 Captive populations in support of conservation

There were some notable early successes in maintaining captive populations in zoos of species that had become extinct in the wild. These successes, with species such as Przewalski's horse *Equus ferus przewalskii*[12] (current IUCN Red List status: endangered) (**Fig. 10.7**) and Père David's deer *Elaphurus davidianus* (current IUCN Red List status: extinct in the wild), were relatively unplanned by modern standards (see **Box 10.2**), but indicated the potential of zoos as arks to help save species from extinction.

[12] The nomenclature for Przewalski's horse is debated; some authors give *Equus caballus przewalskii,* whereas other sources give *Equus ferus przelwalskii*.

What is not under debate is that this species of wild equid has been saved from extinction by captive breeding in zoos.

Box 10.2 SAVED FROM EXTINCTION: ACCIDENT OR PLANNING?

There are several species of animal that are extinct in the wild, but still exist in captivity. One of the most famous is Père David's deer, or milu, *Elaphurus davidianus* (**Fig. 10.8**), originally from the marshes of Central China but probably already extinct in the wild two or three thousand years ago (Whitehead 1972). When Père Armand David 'discovered' the milu for Western science, it only existed in captivity inside the Imperial Hunting Park in Peking (now Beijing). This herd was exterminated at the end of the nineteenth century when the wall of the park was breached by floods and the deer were eaten, with the last few being killed during the 1900 Boxer Rebellion. Luckily, the Duke of Bedford kept a small group of milu in the grounds of Woburn Abbey and, realizing the plight of the species, he managed to assemble a group of eighteen, drawn from his own park and other European zoos. These eighteen are the **founders** of all milu alive today.

The species bred well in captivity, with about a thousand animals alive at the start of the 1980s (Cherfas 1984), distributed among a number of different zoos. By the 1980s, it was possible to start reintroducing milu into the wild in China—firstly, into the Beijing Milu Park (in 1985), and subsequently into the Dafeng Natural Reserve (in 1986), in both of which areas the herd has subsequently grown (Hu and Jiang 2002).

Surprisingly, analysis of the records of 2,042 individuals born between 1947 and 2000 shows that there is relatively little **inbreeding** (Sternicki *et al.* 2003). This seems almost the perfect example of a species, extinct in the wild, being maintained in zoos and eventually reintroduced back into its former range. In retrospect, however, it is probably only good luck that some specimens were available to form a founder herd, that there was someone with the vision to form the founder herd, and that the subsequent descendants are not too troubled with inbreeding.

Other species for which the last surviving members also lived in zoos—such as the quagga, the passenger pigeon, and the thylacine, were not quite so lucky—and became extinct.

Figure 10.8 Père David's deer *Elaphurus davidianus* was already extinct in the wild long before it became known to Western science. A small number of captive animals were the ancestors of the modern population and, recently, the species has been reintroduced back to China. (Photograph: Geoff Hosey)

Much of the work on quantifying this role (that is, on identifying just how much saving of species zoos could do and formulating the underlying theoretical basis of captive management (that is, how to manage small fragmented populations) was carried out during the 1970s and 1980s (e.g. Foose 1980; Mace 1986).

The WZCS (IUDZG/BSG 1993) pointed out that captive animals represented an important part of the remaining **gene pool** for some species and that, because of this, captive management was probably the only option for maintaining stocks of critically endangered species. The role of the zoo gene pool was to supplement wild populations, or to build entirely new ones (for example, through reintroduction), and, to do this, the gene pool had to be managed through cooperative effort.

More details on how zoos manage these gene pools are given in **Chapter 9**. Here, it is worth looking more closely at the scope of the problem in terms of how many species zoos are likely to be able to save and how zoos should select the species on which they focus their attention.

10.3.2 How many species can be saved in zoos?

We saw earlier in this chapter that the IUCN has identified 7,250 species of vertebrates, and 3,570 species of invertebrates that are threatened in the wild (IUCN 2012). How many of these can be saved from extinction by captive management in zoos?

Over 20 years ago it was estimated (Seal 1991) that about a thousand zoos worldwide that are likely to be involved in cooperative breeding programmes may have about 500,000 spaces for animals. Although the spaces available will be limited in terms of the animals for which they are suitable, nevertheless this seems a reasonable number of spaces—but is it enough?

Unfortunately, the answer is probably 'no'. Maintaining captive populations of rare species involves a lot more than simply putting animals together and waiting for them to breed. As we

saw in **Chapter 9**, captive populations are usually small and fragmented, so maintaining **genetic diversity** and avoiding the problems of inbreeding are real problems. Thus, we have the proposal, now encapsulated in WZCS and WZACS, that the goal of small population management should be the maintenance of 90 per cent of the genetic variation of the wild population for a period of 100–200 years (Soulé *et al.* 1986). To do this requires an effective captive population (see **Chapter 9**) of about 200–250 animals for each species, depending on a variety of different variables, including life history traits and the genetic make-up of the population.

In this case, there is space for about 2,000 species, provided that the spaces are used with 100 per cent efficiency (Seal 1991). Of course, different kinds of animal need different amounts and types of space, so evaluations of space (both available and needed) are perhaps better undertaken at class or order level. For example, a survey of North American zoos indicated that sixteen snake species could be accommodated in captive management programmes in the forty-four zoos that responded to the survey (Quinn and Quinn 1993). A similar survey of spaces for birds concluded that fewer than 141 long-term management programmes could be accommodated (Sheppard 1995). Similar space surveys are regularly done by zoo associations so that they have an idea of how much space there is, and can produce regional collection plans (see **Chapter 9**). However, although there are more zoos now, it is likely that they hold fewer species than was thought 20 years ago, so the space situation is probably worse now.

On a more positive note, for threatened species of amphibians, if each of the zoos represented in the current accredited programmes were to take responsibility for maintaining a captive population of just five species, then, to quote Dickie *et al.* (2007), '*it is possible that zoos could be instrumental in saving an entire group of vertebrates*'. (See **Box 10.3** for more about how zoos are saving amphibians.)

In some ways, this sort of analysis identifies only the minimum that can be achieved.

Box 10.3 SAVING THE AMPHIBIANS FROM OBLIVION

In the case of the amphibians, we have very nearly a whole class of animals in danger of extinction (**Fig. 10.9**). Some assessments suggest that 1,856 species, representing 32 per cent of the known species in the world, are threatened with imminent extinction and as many as 168 species may have become extinct during the past two decades (Stuart *et al.* 2004).

A major problem for these animals is their susceptibility to infection with a pathogenic chytrid fungus (see **section 11.5.4**), and this epidemic is going to worsen because of the effects of global warming (Pounds *et al.* 2006). But they also suffer from other threats, including habitat loss and exploitation, and those species with small geographical ranges are particularly at risk (Sodhi *et al.* 2008) (**Fig. 10.10**).

So what can zoos do to help save the amphibians? Amphibians are relatively small animals; they also have high **fecundity**, low maintenance costs, and show few behavioural problems in captivity, all of which means that zoos could have a valuable role to play in their conservation (Bloxam and Tonge 1995). The Amphibian Specialist Group (ASG) of IUCN/SSC has produced a conservation action plan for these animals (Gascon *et al.* 2007), available online at **http://www.amphibians.org**, which includes captive breeding, some of which is to be achieved in zoos. Recently, ASG has joined with WAZA and other regional zoo associations to form an Amphibian Ark (AArk) to coordinate *ex situ* conservation of as many amphibian species as possible and designated 2008 as the 'Year of the Frog' (see **Box 10.5**).

Figure 10.9 The giant ditch frog *Leptodactylus fallax*, also known as the mountain chicken. This species epitomizes the current plight of the amphibians. It has been subject to severe habitat loss, human predation for food (hence its common name), and now chytridiomycosis, and is listed by IUCN as critically endangered. Its future survival probably depends upon captive management. (Photograph: Geoff Hosey)
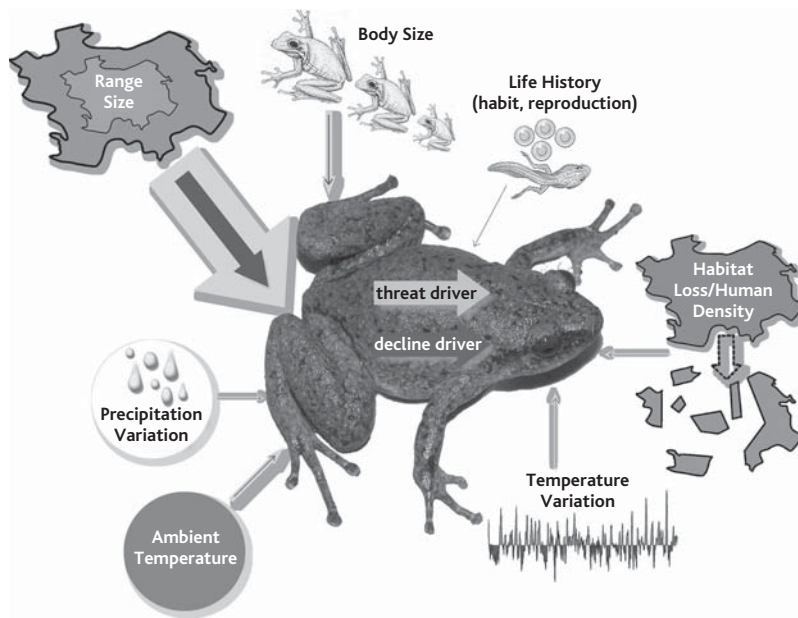
Figure 10.10 Recent studies have highlighted that many amphibians are on the brink of extinction because of various threats to their survival, including major ecological changes (indicated by light arrows) and an inability to survive in the resulting habitat (indicated by dark arrows) because some of their life history traits are no longer appropriate in their environment. The thickness of the arrows indicates the amount of risk that these variables present; for example, small range size is a greater predictor of risk and decline than other environmental and life history variables. (From Sodhi *et al.* 2008)

Let us look at one example: the blue poison dart frog *Dendrobates azureus* (**Plate 10.1**). This species is endemic to a few isolated areas in Suriname in South America, where it is threatened with extinction. Captive breeding has helped to boost the zoo population of these frogs to 175 first-generation captive-bred animals in twenty AZA institutions, with fourteen of the original twenty wild-caught founders still reproductive (**http://www.amphibiaweb.org**). A **studbook** for this species is held by EAZA, and European zoos are also involved in its captive breeding.

Hopefully, this sort of coordinated action will help save many more amphibian species before it is too late.

The WZCS points out that more spaces could be made available by, for example, reallocating spaces that are currently taken up by animals that are not actively contributing to a management programme, such as old animals, hybrids, and those of low genetic value (Melfi 2012b), and/or by encouraging many of the smaller zoos that are not part of the international breeding programmes to become involved. Furthermore, not all species will need even a hundred years of occupation of zoo space, and maintaining a large self-sustaining *ex situ* population may only be necessary for the most severely endangered species; for less endangered species, smaller zoo populations could serve as a reserve in case of problems with the wild populations.

10.3.3 Which species should be saved?

Given that there are not enough spaces to keep self-sustaining populations of all endangered species, then clearly some prioritization is necessary.

In the WZACS, several criteria are listed as aids to this prioritization.

- How threatened are the wild populations?
- How unique is the species taxonomically?
- Is the species native to the region?
- Are there established and successful husbandry protocols already in place?
- Is there already a captive population?
- Could the species be regarded as a 'flagship' species?
- Does the species have additional educational or research value?

Setting the priorities is achieved through IUCN, zoo specialist groups, non-governmental organizations (NGOs), and conservation strategies such as 'Zero Extinctions' and 'Biodiversity Hotspots' (Myers *et al.* 2000; Wilson *et al.* 2005; Bottrill *et al.* 2008 (see **Chapter 9**).

One view that has been given by Balmford *et al.* (1996) is that current population management programmes are biased in favour of mammals and that, even among mammals, more attention is given to larger-bodied species. They suggest that a more realistic approach would be to concentrate on smaller-bodied animals, which are cheaper to maintain in captivity, use less space, and are not necessarily less popular with the visiting public.

However, some support for the current zoo bias in favour of the **charismatic megafauna**[13] is provided by Cardillo *et al.* (2005), who demonstrate that extinction risk rises sharply for animals with a body weight above a threshold of 3 kg. For example, in the current (since 2011) EAZA/IUCN/SSC Southeast Asia campaign, mammals over 1 kg in body weight are identified as most at risk. This suggests that the future loss of biodiversity among large mammals could be far more rapid than expected.

Another view (Hutchins *et al.* 1995) is that zoos should concentrate on flagship species—that is, those species that can excite public attention (golden lion tamarins *Leontopithecus rosalia* and gorillas *Gorilla* spp. are often quoted as examples of flagship species), because this can also raise public support and perhaps generate funds for *in situ* conservation which can benefit many more species. Zoos are probably better at a species-conservation approach than a habitat-conservation approach because keeping species is what they do, and this approach would favour the idea of flagship species.

10.3.4 Species or subspecies?

A further problem for zoos is that of deciding at what **taxonomic** level captive breeding plans should be put in place. As Mace (2004) has pointed out, taxonomy and conservation go hand in hand. The basis of much conservation planning is the species list (for example, the IUCN Red List), but if the taxonomic unit of choice is the species, then we are still faced with decisions about what constitutes a particular species, because definitions are not easy to apply in many cases. (See **Chapter 5** for more discussion of this.)

Not only is our knowledge of the total number of species on Earth poor—perhaps 1.7 million out of between 7 million and 15 million species (see Mace 2004)—but what we think we do know is liable to change. For example, Roca *et al.* (2001) provide genetic evidence that two species of African elephant should now be recognized, with forest elephants *Loxodonta cyclotis* now classified as distinct from the savannah elephant *Loxodonta africana*. The debate over what is or is not a separate species has even extended to the polar bear *Ursus maritimus*. Analysis of the mitochondrial DNA (mtDNA) of polar bears and brown bears *Ursus arctos* suggests

---

[13] The so-called **charismatic megafauna** are the large vertebrates that are disproportionately popular with the general public, from giant pandas, to polar bears, tigers, and elephants. The authors' favourite suggestion for a generic term for the very many species not included in the usual list of charismatic megafauna is 'the other 99.99 per cent'.

that some populations of brown bears are more closely related to polar bears than to other populations of brown bears (Waits *et al.* 1998), which raises questions about their species status (Marris 2007).

Furthermore, many species consist of a number of geographically separate (allopatric) populations that are distinctive enough to be regarded as subspecies.

So, should different subspecies be maintained as separate captive populations? Until about 30 years ago, different subspecies were routinely allowed to hybridize in zoos, usually inadvertently simply because there was less knowledge of the differences between species. For example, **Fig. 10.11** shows a hybrid of black-and-white and red ruffed lemurs in a zoo in the 1980s; at that time, the two **taxa** were considered to be subspecies of the same species, but modern thinking is that the two are distinct species: *Varecia variegata* and *Varecia rubra* (Vasey and Tattersall 2002). Luckily, zoos have maintained these two taxa as separate populations in the last 25 years, because each looks so distinctive, but

this does illustrate the difficulties in prioritizing taxonomic levels.

The advent of modern molecular techniques has provided some help in identifying the evolutionary distinctiveness of different populations (Wayne *et al.* 1994). For example, African hunting dogs *Lycaon pictus* from southern and eastern areas of Africa look similar to each other, but, on the basis of mtDNA sequences, these two populations are dissimilar enough to warrant subspecies classification. The recommendation is that, in captive breeding and reintroduction programmes, the two populations should be kept separate (Wayne *et al.* 1994).

In Sumatran rhinoceros *Dicerorhinus sumatrensis* (**Fig. 10.12**), on the other hand, mtDNA analysis of geographically separate populations from West Malaysia, Sumatra, and Borneo showed that the differences between these populations were slight enough to recommend that the appropriate taxonomic unit for conservation was the species, rather than the local populations (Amato *et al.* 1995). (See **Box 10.4** for more information about the analysis of mtDNA.)

Figure 10.11 The taxonomy of animals has changed over time (see **section 5.2.2**) and, coupled with previously misidentified animals, this has led to the creation of hybrids. This is a hybrid of a red ruffed lemur and a black-and-white ruffed lemur, photographed in the 1980s. These two kinds of lemur are now considered to be distinct species (*Varecia rubra* and *V.variegata*, respectively) and are managed in such a way as to prevent breeding between the two. (Photograph: Geoff Hosey)

Figure 10.12 The critically endangered Sumatran rhinoceros *Dicerorhinus sumatrensis*, now only found in small numbers in Indonesia and Malaysia. DNA analysis shows these separate populations to be genetically similar. (Photograph: Jeroen Stevens)

Note that, in the two examples just given, the molecular evidence is being used not primarily (if at all) to decide on the taxonomy of the species being studied, but rather as an aid in deciding what the significant population unit should be for conservation purposes. This idea is based on the notion of an **evolutionarily significant unit (ESU)**, which was originally formulated by Ryder (1986) to help to decide on appropriate conservation units below the species level. He defined ESUs as '*populations that actually represent significant adaptive variation based on concordance between sets of data derived by different techniques*'. In other words, genetic diversity between different populations of the same species was a more appropriate criterion for conservation decisions than formal taxonomy.

Obviously, molecular techniques are again invaluable; indeed, some authors came to define the ESU in terms of molecular criteria. Moritz (1994), for example, defined ESUs as '*populations that are reciprocally monophyletic*[14] *for mtDNA* **alleles** *and show significant divergence of allele frequencies at nuclear loci*'.

---

[14] **Monophyletic** refers to any group of taxa that have evolved from a common ancestor.

Box 10.4 THE USE OF MITOCHONDRIAL DNA IN CONSERVATION BIOLOGY

Mitochondrial DNA (mtDNA) is, as its name suggests, DNA that is found in the mitochondria of cells. It is a simple short loop of DNA that is distinct from the DNA of the cell nucleus in two main ways.

1. It replicates via mitosis, not meiosis, so does not undergo the same 'mixing' of genetic material that occurs in nuclear DNA during recombination. Thus, the inheritance of mtDNA is essentially clonal, with mtDNA passed on virtually unchanged from parent to offspring.

2. mtDNA is nearly always inherited only through the maternal line or matrilineage, via the cytoplasm of the egg or ovum (sperm usually contribute almost nothing but nuclear DNA to the newly fertilized egg or zygote).

Although the mtDNA that is passed on from a mother to her offspring is a copy of her mtDNA, it does not always remain completely unchanged. A feature of mtDNA that makes it particularly useful to conservation biologists is that it undergoes mutation at a markedly higher rate than nuclear DNA. This means that mtDNA, in mammals at least, shows a rapid rate of differentiation among populations in comparison with nuclear DNA (Cronin 1993).

Conservation biologists can look at mtDNA sequences from different animals and assess the extent to which it has diverged. This provides an estimate of taxonomic relatedness, either between different species or between different populations of the same species.

Most recent textbooks on conservation biology will have information about the use of both mtDNA and nuclear genetic material to support conservation.
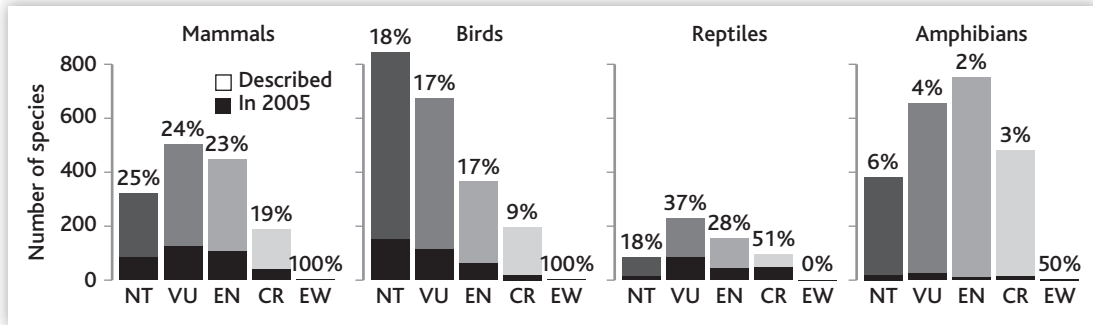
Figure 10.13 The number of species which have been assessed and given an IUCN status classification, together with the number that are housed in ISIS zoos (shaded portion). This looks more optimistic than some assessments, although amphibians are clearly under-represented (Adapted from Conde *et al.* 2011)

Most authors today view ecological and molecular data as being equally important in defining ESUs (Crandall *et al.* 2000; Fraser and Bernatchez 2001).

10.3.5 How well is the ark doing?

As with so many important questions, the answer to this depends partly on who you ask and partly on what you ask. Twenty years ago the answer was that the ark wasn't doing very well at all. An analysis by Rahbeck (1993) showed that 878 zoos worldwide held more than 20,000 specimens of only 140 threatened mammalian species, and that only twenty species were held in numbers sufficient for a viable population. Data from 12 years later didn't look much better, with 417 world zoos holding an average of about sixteen rare species, each with about 100 specimens (Fa *et al.* 2011). This gave a total of ninety species with populations of more than 100, and sixty-four of these were mammals. However, if 'threatened' (i.e. the three IUCN categories together of 'vulnerable', 'endangered', and 'critically endangered') and 'near threatened' are combined, then between a fifth and a quarter of endangered species are represented in ISIS zoos (Conde *et al.* 2011), which looks somewhat better (**Fig.10.13**). Nevertheless, it does seem to be the case that many zoos concentrate, not on species which are endangered, but on species which breed well in captivity,

which the zoo perceives to be most popular with the public (Fa *et al.* 2011), or even those which are seen as most attractive (Frynta *et al.* 2010).

Equally worrying is the finding that so few captive populations are self-sustaining. A recent survey of thirty-one carnivore, thirty-seven primate, twelve ungulate, and seven rodent populations in European and North American zoos found that only 48 per cent are breeding to replacement and only 55 per cent currently retain gene diversity at levels that are recommended (Lees and Wilcken 2009). Other surveys also conclude that many existing captive management programmes will not reach the genetic and demographic goals formulated for them (Leus *et al.* 2011).

It is difficult to know how to interpret these surveys. At first sight they appear to suggest that zoos are generally failing in their mission to be an important part of conservation. Yet we are also aware that there are species still in existence which would either be extinct or else in imminent danger of extinction if it were not for the efforts of zoos in managing *ex situ* populations.[15] Perhaps for now we might conclude that zoos are doing fairly well, but could do a lot better. Indeed, they *must* do better if they are to help save species from extinction (Conway 2011). Amongst other things this probably means better collaboration between zoos as well as between zoos, conservation NGOs,

---

[15] BIAZA has published a list of the top ten species reliant on zoos for their existence (available at http://www.biaza.org which includes species such as the white-clawed crayfish *Austropotamobius pallipes*, the

mountain chicken *Leptodactylus fallax* (**Fig. 10.9**), the blue-crowned laughing thrush *Garrulax courtoisi*, and the Potosi pupfish *Cyprinodon alvarezi*, as well as *Partula* snails (see **Box 10.1**).

and wildlife parks, more emphasis by zoos on conservation activities, additional attention to the biological features of different species (such as group size and composition) to achieve more sustainable populations, and greater specialization on those species most in need of conservation help (Conway 2011, Pritchard et al. 2012).

10.4 Zoos and *in situ* conservation

So far, we have considered the role of zoos in biodiversity conservation in terms of captive management of endangered species, and we have also mentioned a role for zoos in conservation research and education. In fact, these are only convenient labels to apply to a range of conservation-related activities in which zoos are involved. For example, we have used 'education' to cover such diverse things as increasing knowledge, creating empathy, and shaping a positive attitude. Each of these tasks can itself be approached in a number of ways. Similarly, many zoos may be as involved in research on wild-living animals in their natural habitats as they are with that on captive animals. Bringing all these things together involves a coordinated approach, whereby different aspects of the zoo's conservation work are integrated with each other and with the external agencies that are also involved in conservation.

10.4.1 An integrated approach to conservation

The idea of an integrated approach to conservation is not new. More than 15 years ago, in the book *Creative Conservation: Interactive Management of Wild and Captive Animals* (Olney *et al.* 1994), representatives from zoos and conservation organizations around the world were calling for an integrated approach to managing endangered species.

The integrated approach to conservation is highlighted in the WZACS, which distinguishes between 'internal' and 'external' integrated conservation. Internal integrated conservation is not only about keeping animals and providing an enjoyable and informative visitor experience,

but is also about making links between the various activities that contribute to these. These links can include embracing sustainability in the zoo's operation, selling crafts from areas with which the zoo has field conservation links, and informing people about the links between the exhibits and the field research and conservation in which the zoo is involved. External integrated conservation is about forming links with other agencies to promote field conservation, supporting research on wild populations, and raising money to support *in situ* conservation. Of course, not all zoos will do all of these things, but what the integrated approach is advocating is the most effective use of the zoo's resources in achieving conservation objectives.

In practice this means that zoos may financially support *in situ* conservation projects or lend other kinds of support, generate funds through targeted campaigns, be part of *in situ* conservation projects which also involve the captive population, or undertake a host of other activities both within and outside the zoo. For example, WAZA lists a number of projects that their member zoos are involved in (WAZA 2012), which include conservation of the mountain nyala *Tragelaphus buxtoni* in Ethiopia, supporting the Ivoloina Conservation and education Centre in Madagascar, sustainable management of a protected area in the Cardamom Mountains, Cambodia, and the assessment of disease risks of birds on the Galapagos Islands. WAZA also promotes attention raising and fund generation through annual campaigns in its member zoos, and these recently have included 'Year of the frog' (2008), 'Year of the gorilla' (2009), and currently 'Year of the bat' (2011–2012). Other zoo associations have similar campaigns (see **Box 10.5**).

10.4.2 Reintroduction

One of the key goals of many captive management programmes is the eventual reintroduction of species back into the wild. As we have already seen, however, not all species maintained in zoos are part of coordinated programmes that are expected to lead to reintroduction; furthermore, not all individuals

that are part of captive management programmes which include reintroduction will themselves be reintroduced (see **Chapter 9**). It is probably also worth pointing out here that reintroduction for most species is an event that is most likely to occur far into the future, simply because the criteria for successful reintroduction (see below) are not currently satisfied. For all these reasons, the number of successful reintroductions of zoo-born animals is actually quite low at the moment, but there have been some notable successes which give cause for optimism about the prospects of other species in the future. Reintroduction features prominently in both the WZCS and the WZACS, and usually requires the zoo(s) to be involved collaboratively with other conservation agencies.

What is 'reintroduction'?

Of course, there is a long history of animals (and plants too, come to that) being moved around the planet into new habitats through human agency. So what exactly do we mean by 'reintroduction'?

In 1987, the IUCN defined three different types of translocation that could occur through human agency, and these are the definitions generally adopted by the conservation community.

> *Introduction*: intentional or accidental dispersal by human agency of a living organism outside its historically known home range.
>
> *Reintroduction*: intentional movement of an organism into a part of its native range from which it disappeared or became extirpated in historic times as a result of human activity or natural catastrophe.
>
> *Restocking*: movement of numbers of plants or animals of a species with the intention of building up the number of individuals of that species in an original habitat.
>
> (Stuart 1991)

The first of these, introduction, is clearly something to be avoided. Many species of island bird, for example, have been rendered endangered or extinct because of non-native fauna introduced to the islands by man (Halliday 1978).

It is reintroduction and restocking with which zoos and other conservation agencies are concerned.

How necessary is reintroduction?

Most individuals and organizations involved in conservation are agreed that populations of endangered species are best maintained *in situ*; this requires habitat conservation and management, which is beneficial to other species as well and is often relatively less expensive than captive management with subsequent reintroduction. Furthermore, translocation of animals from one place to another in the wild has a higher success rate than trying to establish self-sustaining wild populations of captive-bred animals (Stanley Price 1991).

So why should reintroduction be done at all? To put this into some kind of perspective, only sixty-eight species were recommended for reintroduction in IUCN/SSC action plans by the end of 1992, and captive breeding was also recommended for forty-five of these species (Wilson and Stanley Price 1994). However, the database of the Reintroduction Specialist Group (RSG) of the Species Survival Commission (SSC) of the IUCN listed 149 past, current, and proposed bird and mammal reintroduction projects, involving 121 species (Wilson and Stanley Price 1994).

This does not seem very many, so why are there so few? The answer generally, as already mentioned, is that the criteria that need to be satisfied for reintroduction (see next section) are not satisfied. Nevertheless, reintroduction, where feasible, is considered worthwhile because there are public awareness spin-offs and because some species will not survive at all otherwise. With better habitat restoration and the use of gene technologies in the future, prospects for reintroduction may well improve (Stuart 1991).

10.4.3 The criteria for reintroduction

Establishing new self-sustaining populations of endangered species in areas where they have become extinct is clearly not likely to be an easy task, and a number of general criteria have been used to help to decide whether or not reintroduction is

feasible. These criteria are discussed more fully by Kleiman *et al.* (1994) and include the following.

1. There should be a need to augment the size or genetic diversity of the wild population.

2. There should be available and appropriate stock to use in the reintroduction.

3. There should not be any jeopardy to the existing wild population.

4. The original causes of the species' decline should have been removed.

5. There should be sufficient appropriate and protected habitat within the species' former range.

6. The available habitat should have no members of the species (reintroduction) or only a sparse population (restocking).

7. There should be no major negative impact on the local human population.

8. There should be local community support for the reintroduction.

9. There should be support from relevant governmental and non-governmental organizations.

10. The reintroduction should conform to relevant laws and regulations.

11. The reintroduction technique should be known.

12. There should be sufficient knowledge of the species' biology.

13. There should be sufficient resources for the reintroduction.

In 1995, the IUCN approved reintroduction guidelines produced by the SSC Reintroduction Specialist Group (see **section 3.2.4**), which are available to view on the IUCN website (see **Websites and other resources**).

10.4.4 How are zoos involved in reintroduction?

Of course, the animals used in reintroduction projects may not have come from zoos; indeed, they may not even be captive born. So, to what extent are zoo animals involved in reintroduction projects? The answer, at the moment, is that they are involved rather less than we would expect. Of 129 reintroduction projects surveyed by Beck *et al.* (1994), seventy-six (59 per cent) used zoo-bred animals or their descendants. This involved a minimum of 20,849 individual animals (1,958 mammals; 8,271 birds; 10,620 reptiles and amphibians), which, as the authors point out, is about the equivalent of the collections of only three or four major zoos combined. This may not seem very many, but it is worth remembering that the aim of the captive management programme is to maintain 90 per cent of genetic diversity of those species that are part of the programme for at least 100 years. The assumption behind this is that reintroduction programmes will not be feasible for most species until well into the future. At the moment, there are still sufficient wild stocks in other parts of their range for some of the species in reintroduction programmes, and many of the species involved in these programmes are not the most severely endangered. But it is very unlikely that this will be the case in the future.

10.4.5 Some examples of reintroduction projects

Several reintroduction projects have become particularly well known, partly because of the intensiveness of monitoring that has accompanied them and partly because the animals have been regarded as flagship species, whose importance to conservation goes beyond just being a saved species.

Perhaps the best known is the reintroduction programme for the golden lion tamarin *Leontopithecus rosalia* (**Plate 10.2**) back into the Atlantic Coast rainforest of Brazil (Kleiman *et al.* 1986; Stoinski *et al.* 1997). These small primates were severely endangered in the wild and in captivity (where **mortality** rates were exceeding **birth rates** in the 1980s), and the first step in their conservation programme was to identify what was amiss with their captive management and rectify it. As a result, a self-sustaining captive population was

built up at the Smithsonian's National Zoo in Washington, DC, and in other zoos, in association with a primate centre in Rio de Janeiro.

Before reintroduction was attempted, the animals went through a pre-release training programme during which they learned how to search for hidden food and how to use natural substrates for locomotion. The tamarins were subsequently acclimatized in cages built around natural vegetation at the release site.

The initial set of released animals (fourteen in 1984) fared badly, and a year later eleven of them had either died or been removed (Stoinski *et al.* 1997). In response to this, the training programme was improved—in particular, with a greater emphasis on post-release training—and this led to more successful reintroduction (a reintroduced population of 169 animals, constituting 23 per cent of the wild population, by 1995). Importantly, wild-born tamarins had far better locomotory and foraging skills than their captive-born counterparts, so giving birth in the wild is of great importance for reintroduced animals (Stoinski *et al.* 2003). The lion tamarin programme is now seen as a success (Kierulff *et al.* 2012).

In the example of the golden lion tamarins, the captive-born animals were being reintroduced to supplement an existing, although threatened, wild population. A slightly different case is presented by the Arabian oryx *Oryx leucoryx* (**Fig. 10.14**) because this species was extinct in the wild, so the reintroduced animals were part of a programme to establish a wild population where none existed.

This species was exterminated in the wild by 1972, but a captive herd had been established before this. Reintroduction was successfully accomplished to a reserve in Oman in 1982 and again in 1984, leading to the growth of an independent population that numbered about 280 animals by October 1995, using over 16,000km^2 of the reserve area (Spalton *et al.* 1999). Unfortunately, poaching, which was the main cause of extinction in the first place, started again in 1996 so that, by September 1998, only 138 animals were

Figure 10.14 The Arabian oryx *Oryx leucoryx* pictured here was considered extinct in the wild by 1972; several attempts have subsequently been made to reintroduce animals into Oman and, more recently, Saudi Arabia. (Photograph: Geoff Hosey)

left, of which only twenty-eight were females. As a result, as many as possible of the remaining animals were caught and brought back into captivity. Similar reintroduction of the oryx is being carried out in Saudi Arabia and this promises to be more successful (Ostrowski *et al.* 1998).

Slightly different is the case of the Californian condor *Gymnogyps californianus* (**Fig. 10.15**) because, here, the last remaining wild specimens were brought into captivity to ensure the survival of a species that was seen as doomed in the wild. This species had been rare for many years, but, by 1985, the total wild population numbered only fifteen birds (Toone and Wallace 1994). Between 1986 and 1987, all the remaining wild condors were brought into captivity in Los Angeles Zoo and San Diego Wild Animal Park. By 1994, forty-nine condors had been bred at these two zoos;

release back into the wild started in 1992. Mortality in the wild continued to be a cause for concern, however, with some birds colliding with overhead power cables and others contracting lead poisoning from eating bullet fragments in carcasses (Meretsky *et al.* 2000), so the viability of a wild population remains unclear.

These examples, and one or two others like the red wolf *Canis lupus rufus* and the black-footed ferret *Mustela nigripes*, are often quoted as reintroduction success stories, and they have a high profile partly because they involved iconic species which were either extinct or almost extinct in the wild, but also because they have been comprehensively monitored, researched, and documented. However, the reality is that comparatively few reintroductions have been successfully attempted and the technique is not a common part of

Figure 10.15 Attempts made to save the extremely rare Californian condor *Gymnogyps californianus* (a) through captive breeding have resulted in the development of a complex rearing process for the captive-bred chicks, which involves the chick being fed by a puppet (b), representing the head of an adult condor, to help it imprint correctly and learn its appropriate species identity. (Photographs: (a) Scott Frier © US Fish & Wildlife Service; (b) Ron Garrison © US Fish & Wildlife Service)

Box 10.5 EAZA CAMPAIGNS

Raising awareness, promoting behavioural change, changing legislation, and fundraising to support conservation projects are important ways in which zoos can contribute to international conservation efforts. For several years, EAZA has mounted fundraising campaigns targeted at a particular key project, as part of which member zoos attempt to raise money by holding special events, activities, and exhibitions. In 2002–2003 and 2003–2004, the campaign was to support tiger conservation by providing funding towards nine different tiger projects in Russia, Indonesia, Thailand, and India. This was followed in 2004–2005 by 'Shellshock', the EAZA Turtle and Tortoise campaign, which aimed to raise public awareness about the threats faced by these animals, to promote captive breeding of some of the thirty-six most endangered species, and to raise €150,000 to support turtle and tortoise conservation.

The 2005–2006 campaign was 'Save the Rhinos'. Its aims were, again, to raise public awareness of the threats to rhinoceros populations and to raise funds (a goal of €350,000) to support conservation projects within rhino range countries. Save the Rhinos was followed in 2006–2007 by EAZA's Madagascar campaign (**Fig. 10.16**) and, in 2008, EAZA linked with AZA and other zoo organizations in a global campaign 'The Year of the Frog' (see **http://www.yearofthefrog.org/**). Since then there have been European carnivore (2008–2010) and ape (2011) campaigns, one of

the outcomes of which was that in the EU palm oil must be labelled on all products. Since the launch of their campaigns in 2000 EAZA has raised more than €3.8 million through its member zoos, which has been distributed to more than 100 conservation projects worldwide.

EAZA sets specific targets for its conservation campaigns, both in terms of funds raised and other activities, such as raising awareness. The Shellshock campaign, for example, involved 119 EAZA member institutions and also thirteen non-EAZA organizations—notably including the Chinese Association of Zoological Gardens (CAZG). The decision by the CAZG to adopt the Shellshock campaign, and to develop its own long-term turtle and tortoise conservation campaign (under the title 'Careshell'), has the potential for a significant impact in an area of the world in which large numbers of turtles and tortoises are routinely killed for consumption and medicinal purposes.

The final total for funds raised by Shellshock was over €370,000, more than double the initial target of €150,000. In consultation with the Turtle Conservation Fund (TCF) and the Marine Turtle Research Group (MTRG), Shellshock funds have been distributed to a number of *in situ* turtle and tortoise conservation projects worldwide, from Cambodia and Vietnam to the Philippines.

Further details about Shellshock and other EAZA campaigns can be found online at **http://www.eaza.net**

Figure 10.16 Madagascar was the subject of the EAZA awareness campaign in 2006–2007, in which EAZA member zoos highlighted conservation issues to their zoo visitors and aimed to raise funds to support conservation activities *in situ*, as illustrated here at Apenheul Primate Park in the Netherlands. (Photograph: Sheila Pankhurst)

conservation practice (Stanley Price and Fa 2007). Those reintroductions which are carried out are usually part of an integrated management programme, sometimes to supplement existing wild populations. Examples include captive breeding and reintroduction programmes for the field cricket *Gryllus campestris* and wart-biter bush cricket *Decticus verrucivorus* in the UK (Pearce-Kelly *et al*. 1998), the black-footed rock wallaby *Petrogale lateralis* in South Australia (Muhic *et al*. 2012), and the bearded vulture *Gypaetus barbatus* in the European Alps (Bustamante 1996).

Is reintroduction good value for money?

The golden lion tamarin project is very well known and has helped to raise awareness of the conservation of endangered species, but it comes at a price. That price is about US$22,000 for each surviving reintroduced tamarin (Kleiman *et al*. 1991). This amount is made up of about $1,657 per animal per year in maintenance costs at the zoo (keeper time, food, veterinary care, housing, etc.), plus the reintroduction costs—and that is at 1989 prices.

Clearly, both captive management and reintroduction are, at least for this tamarin, costly activities. It has been suggested by Balmford *et al*. (1995) that, for large-bodied species, *in situ* conservation is relatively cheaper than captive propagation, can result in equally good population growth, and has the additional benefit that it helps conserve entire ecosystems and not only the target species. But we should bear in mind that these costs quoted for the tamarin project are probably not typical, and that many other reintroduction projects, particularly those involving native species, are likely to be less costly. Furthermore, it is probably misleading to see captive propagation and *in situ* conservation as alternatives, because, in many cases, both may be needed and, for some species, *in situ* conservation may simply not be an option.

10.4.6 The conservation of native species

As well as having to make decisions on the taxonomic level at which conservation projects are carried out, zoos must decide what priority to give to the conservation of native species on their doorstep as opposed to wild animals from further afield. Species such as sand lizards *Lacerta agilis*, corncrakes *crex crex*,[16] field crickets *Gryllus* spp*.,* and hamsters may lack the immediate visitor appeal of zebras and tigers, but (in most of Europe at least) native species often require relatively little space for housing and are better able to tolerate the local climate. Both Chester Zoo and Marwell Zoo, for example, maintain thriving colonies of captive-bred sand lizards (**Fig. 10.17**). Animals from both zoos have been successfully reintroduced back into selected sites in the UK where there is suitable habitat.Whipsnade Wild Animal Park in Bedfordshire, in collaboration with the Royal Society for the Protection of Birds (RSPB) and English Nature, has been rearing corncrake chicks since 2002 for release back into the wild in the UK, and at London Zoo[17] a captive breeding programme was established in 1991 for the field cricket *Gryllus campestris*, a species listed as 'endangered' on the UK Biodiversity Action Plan (BAP). At Rotterdam Zoo (Diergaarde Blijdorp), a captive breeding facility has been set up for the European hamster *Cricetus cricetus*, a species which became extinct in the wild in the Netherlands but has now been successfully reintroduced at a number of sites (**Fig. 10.18**). Elsewhere in the world many zoos devote attention to native species. At Taronga Zoo, for example, 50 per cent of the captive population is native species, with conservation projects involving species such as the Regent honeyeater *Xanthomysa phrygia*, the brush-tailed rock wallaby *Petrogale penicillata* (**Fig. 10.19**) and the Tasmanian devil *Sarcophilus harrisii* (see **Box 10.6**).

---

[16] The corncrake is a medium-sized brown bird related to the coot and moorhen. Corncrakes favour grassy meadows, but, where they are present, they are usually heard rather than seen, owing to their excellent camouflage.

[17] London Zoo and Whipsnade Wild Animal Park both come under the umbrella of the Zoological Society of London (ZSL). Further information about a range of ZSL conservation initiatives can be found online at **http://www.zsl.org/field-conservation/**

Figure 10.17 The sand lizard *Lacerta agilis* represents a native British species that has been bred successfully in captivity in several zoos and reintroduced back into the wild. (Photograph: Sonja Kuehn)

Figure 10.18 The European hamster *Cricetus cricetus*, which became extinct in the Netherlands, but which has now been successfully reintroduced after a captive management programme. (Photograph: katanski/ CC-BY).

Figure 10.19 The brush-tailed rock wallaby *Petrogale penicillata*, one of several rock wallaby species which have experienced severe declines in Australia, and for which there are now captive management programmes. (Photograph: Geoff Hosey)

Box 10.6 HELPING AN AILING WILD POPULATION: THE TASMANIAN DEVIL

The Tasmanian devil *Sarcophilus harrisii* is the largest living carnivorous marsupial (**Fig.10.20**). At one time, possibly as recently as 3,000 years ago, it was widespread in Australia, but now it is only found on the island of Tasmania. Since 1996 populations on Tasmania have been subject to a devastating disease, devil facial tumour disease (DFTD), which can affect up to 83 per cent of animals trapped at any particular site (Hawkins *et al.* 2006) (**Fig. 10.21**). The disease appears to be a rogue cell line which evolved in a tumour, and the devils' immune systems are unable to recognize it as non-self because their immune systems are compromised by low genetic diversity (Woods *et al.* 2007). DFTD is a contagious cancer, and appears to be transmitted from one animal to another through biting.

In situ conservation measures include the trapping and removal of infected animals in an attempt to limit the spread of the disease, but because the survival of the species in the wild is in such doubt a captive population of healthy animals is being established in a number of Australian zoos (Jones *et al.* 2007). This will provide an insurance population in case the wild population fails to survive.

Figure 10.20 The Tasmanian devil *Sarcophilus harrisii*, formerly found on mainland Australia as well, but now restricted to Tasmania. (Photograph: Jeroen Stevens)
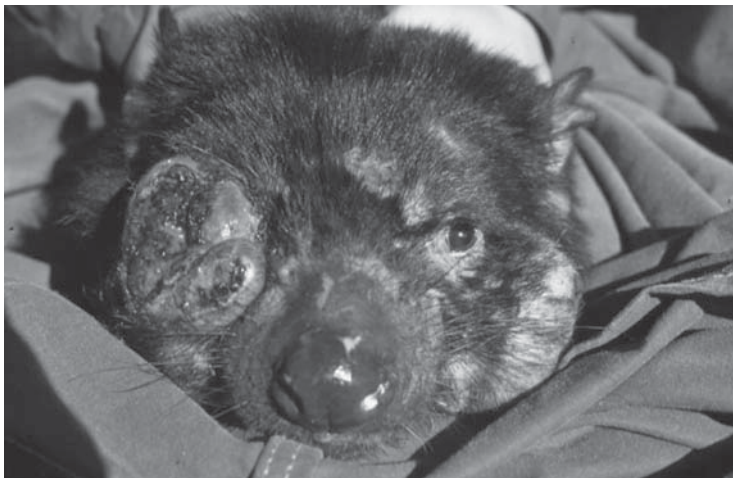
Figure 10.21 Tasmanian devil with facial tumour disease (Photograph: Menna Jones, from McCallum and Jones 2006).

10.5 Conservation of behaviour

Much of the theory and practice of small population management that is implemented in zoos is formulated from a genetic and demographic point of view, and is concerned with the goals of maintaining genetic diversity, avoiding inbreeding, and keeping the shape of the population viable (see **Chapter 9**). There are real issues about potential losses of genetic diversity in small populations (see **section 9.2**), but there is also the possibility that captive animal populations might show genetic adaptation to captivity.

One of the issues here is to avoid domestication (Price 1984), which can happen surprisingly rapidly. For example, farmed silver foxes *Vulpes vulpes* have routinely been selected for tameness, as shown by willingness to be handled and low levels of aggression. After thirty or so generations, these animals show physiological (lower serum cholesterol) and genetic differences, as well as the more obvious behavioural ones, in comparison with unselected foxes (Harri *et al.* 2003; Lindberg *et al.* 2005). This sort of selection is not necessarily a totally negative thing to be avoided at all costs in zoo animals. For example, it has been suggested as appropriate for some common species that are kept for display, but are of no immediate conservation importance, especially if the selection is to maintain a 'classic' species **phenotype** (Frankham *et al.* 1986). But for species of conservation importance it is clearly important to avoid genetic adaptation to captivity by using improved molecular techniques, minimizing the number of generations spent in captivity, and crossing replicate groups within fragmented populations (Frankham 2008; 2010; Williams and Hoffman 2009) (see **Chapter 7**).

However, we should remember that behaviour is influenced not only by genetic variation, but also by **learning** that takes place in the lifetime of the animal. Because of this, it is important to ensure that behavioural diversity is maintained and that key behaviours that are needed for survival in the wild are not lost from the captive population

(Lyles and May 1987; May and Lyles 1987; Festa-Bianchet and Apollonio 2003).

Maintaining behavioural diversity is particularly important for animals that are being reintroduced to the wild, but potential to survive in the wild should be the criterion of success for all captive management programmes (Shepherdson 1994) because, for many species, reintroduction is a long way in the future and the individuals to be reintroduced may not yet have been born. Appropriate environmental enrichment and training are ways in which animals can be prepared for release into the wild. The purpose of this is to ensure that animals destined for release have the **behavioural competence** to be able to survive in the wild (Wielebnowski 1998). We have already seen how golden lion tamarins were put through a pre-release training programme so that they could find hidden food and use natural substrates for locomotion.

One particularly important aspect of developing behavioural competence is in training animals to avoid predators, because an inability to express natural anti-predator behaviours is a major cause of failure in animal reintroductions (Griffin *et al.* 2000). This sort of training is often achieved through **classical conditioning**, in which a predator model is paired with some sort of aversive **stimulus**. This has been used, for example, to train captive-born greater rheas *Rhea americana* at Belo Horizonte Zoo, Brazil, to behave appropriately when confronted by a predator (de Azevedo and Young 2006a; 2006b). The predators themselves may also have problems. Reintroduced captive-born carnivores are less likely to survive than reintroduced wild-caught carnivores, largely because of starvation and unsuccessful predator and competitor avoidance (Jule *et al.* 2008).

We are increasingly coming to realize the contribution that animal temperament makes to the success of these initiatives (McDougall *et al.* 2006; Watters and Meehan 2007). As an example, Bremner Harrison *et al.* (2004) found that captive-bred swift foxes *Vulpes velox* (**Fig. 10.22**) previously assessed as bold were more likely to die in the first six months after release than those rated as shy, presumably because, as in captivity, they had low fear

Figure 10.22 Personality indicators identified in swift foxes *Vulpes velox* reintroduced into the wild were successful predictors of their survival. Animals identified as bold did not survive as well during the first six months after release into the wild as did those assessed as shy. (Photograph: Sheila Pankhurst)

levels and were more likely to approach novel objects (see **Box 4.2** for further discussion of temperament or personality traits in non-human animals).

Maintaining behavioural diversity in animals that are not imminently about to be released is largely achieved through the same sorts of technique, although in this case the goal is often a more general attempt to achieve a behavioural profile seen in the wild (see **Chapter 4**), rather than the acquisition of particular skills in things such as food finding, predator avoidance, and orientation in the environment. There is perhaps a case to be made that more active management of behavioural development should be undertaken in zoos (Rabin 2003).

10.6 How good are zoos at conserving biodiversity?

However you define conservation, the ultimate aim is to have self-sustaining populations in natural ecosystems in the wild. While realizing this aim may be far in the future for many species,

much work is taking place now to move towards this eventual goal. The integrated conservation ideal (see **section 10.4.1**) sees zoos working on a number of fronts in partnership with other agencies to protect habitats and species in the wild.

The answer to the question of how good zoos are at conserving biodiversity is that it depends on the zoo and on what is being measured. This is probably not a very satisfactory answer, but the word 'zoo' encompasses such a wide range of organizations that it is almost impossible to generalize about their achievements, or otherwise, in the conservation of biodiversity. One approach, perhaps, is to look at what some of the most prominent zoos are achieving in terms of conservation and to consider what can be done to bring other zoos up to the same standards. Let us look, for a moment, at the efforts of the Durrell Wildlife Conservation Trust (DWCT) to save the Mauritius pink pigeon. The pink pigeon *Columba meyeri* (**Fig. 10.23**) is one of a number of species facing extinction in the wild that have been bred successfully in captivity at DWCT.

Figure 10.23 The Mauritius pink pigeon *Columba meyeri* represents a species that has been reintroduced successfully into the wild as a consequence of a captive breeding programme that was initiated by Jersey Zoo. (Photograph: Paignton Zoo Environmental Park)

With only ten birds left in the wild by 1991, the pink pigeon nearly went the way of the dodo. Captive breeding of pink pigeons started in 1977 at Jersey Zoo (now DWCT), alongside measures to protect and manage the remaining few birds in their natural habitat. Captive-bred birds have since been successfully released back into the wild and, today, the pink pigeon population on Mauritius numbers some 350 birds, with the species now listed as 'endangered' rather than 'critically endangered' on the IUCN Red List (see **Websites and other resources**).

It is possible that the pink pigeon could have survived in the wild without a captive breeding programme, but it is equally possible that the species could have become extinct. The captive population, now thriving, is both an insurance policy against future threats to this island species, and a reminder to the many thousands of people who visit DWCT each year of the fragility of island habitats and populations.

Looking at this example, it is hard to argue that zoos such as DWCT do not make a useful and substantial contribution to the conservation of biodiversity. Of course, not all zoos are

like DWCT, but more and more modern zoos are aspiring to and achieving the same goals of integrated conservation.

As the example of the pink pigeon shows, conserving species by captive breeding in zoos is not enough. Zoos must also play a role in the conservation of habitats and ecosystems—but how good are they at doing all of this? This is a surprisingly difficult question to answer, mainly because of the sheer diversity of activities that count as conservation, but also because measures of effectiveness are not easy to formulate. Miller *et al.* (2004) identified eight questions that could be asked of zoos to test whether their conservation activities really did contribute towards achieving their mission. The questions included '*Is there a functional conservation department?*' and '*Do exhibits explain and promote conservation efforts?*' Approaches such as this are valuable, but yield qualitative data, which can make comparisons between different activities and zoos more difficult.

More recently, attempts have been made to find quantitative evaluations of the effectiveness of zoos. One study (Leader-Williams *et al.* 2007) compared zoos in 1992–1993 with what they were doing ten years on in 2003, using measures such as the number of threatened species held in coordinated breeding programmes (this had increased), how many belonged to each major taxon (there was still an over-representation of mammals), and where they were located (most zoos were in rich countries). As a study based in the UK, it also looked at the activities in which BIAZA zoos were involved and found that those zoos that were run by a charity had more education staff, undertook more institutional research, had more visitors, and were involved in more *in situ* projects than private or local authority zoos. Their conclusion was that many zoos were not fulfilling the conservation aspirations of WZACS.

Nevertheless, it is difficult to compare quantitatively the variety of different activities in which zoos are involved, particularly when the link between an activity (such as an educational display) and a measurable effect on conservation is such a diffuse one. An attempt to do this has been made

by Mace *et al.* (2007), using what at first looks to be a very straightforward equation:

$$\text{overall impact} = \text{project importance} \\ \times \text{project volume} \\ \times \text{project effect}$$

Fortunately, Mace *et al.* (2007) also give an indication of the sorts of measure that can be used to quantify these variables and then apply them to a pilot analysis of forty-one projects undertaken by UK zoos. The calculated impact scores suggested that those projects that were involved in direct action to enhance habitats were more effective than other sorts, with—perhaps surprisingly—educational and training projects being the least effective. They also found that project impact was correlated with the amount of funding it received, but not with for how long the project lasted.

This kind of analysis provides a tool that may allow zoos to prioritize their conservation initiatives and then measure how well they are doing. But, for the moment, perhaps the most we can say is that the conservation work that zoos do remains patchy and the effectiveness of that work is still relatively unclear.

10.7 Conservation and zoos: looking to the future

Twenty years ago, the maintenance of breeding groups of endangered species to safeguard their future was often seen as the most important way in which zoos could contribute to animal conservation. Now, although captive breeding is still seen as important, it is only one of a number of integrated activities in which zoos are involved and the emphasis has moved much more towards involvement in *in situ* projects. More and more zoos are now making the transition from being 'zoos that undertake conservation' to becoming 'conservation organizations that run zoos' (Zimmermann and Wilkinson 2007). This is concordant with the vision of WZCS and WZACS that zoos should become 'conservation centres',

which would have the following three characteristics (Hatchwell *et al.* 2007).

1. *Bringing about a change in behaviour of zoo visitors and decision-makers*   In the future, zoos should address this by becoming more rigorous in inspiring zoo visitors to care about conservation and measuring their impact in doing this, by defining the highest of standards in animal care and welfare, by becoming involved in conservation locally, and by emphasizing links between humans and biodiversity. Inspiring zoo visitors may result, amongst other things, in them visiting zoos more regularly, and there is evidence from Australia that many zoo visits which are logged as if they are individual events are in fact return visits by regular zoo-goers (Smith 2013).

2. *Establishing links between the* ex situ *work of the zoo and* in situ *conservation activities*   There are many ways in which zoos can achieve this, including fundraising campaigns, providing expertise in small-population management, developing zoo exhibits in parallel with *in situ* projects, and making explicit links between exhibits and field sites. A good example of this is the involvement of zoos and other organizations in the conservation of the critically endangered Sulawesi black macaque *Macaca nigra* (Melfi 2010).

3. *Making direct contributions to* in situ *conservation activities*   Again, there are numerous ways in which zoos can do this, including running their own field projects and raising money for field conservation. Zoos contribute substantial funding to field conservation (Gusset and Dick 2011) (**Fig. 10.24**). For example, the Disney Worldwide Conservation Fund (DWCF), founded in 1995, has since then awarded more than $18 million to projects in 111 countries.

Recently there has been renewed appreciation of the importance of the captive collections to species conservation (Bowkett 2009), partly because of the growing realization that *in situ* conservation will become less of an option for an increasing number of species in future (Conway 2011).
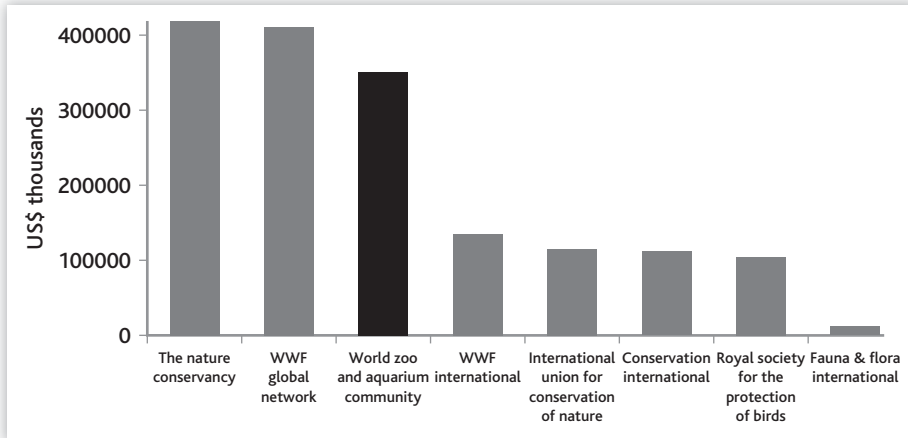
Figure 10.24 The amount of money spent by the world zoo and aquarium community, and by major international conservation organizations, in 2008. (From Gusset and Dick 2011)

In the light of constraints on zoo space, it will be a challenge for zoos to find ways of prioritizing which species are most deserving of help. Overall, these considerations might require zoos to pay some attention both to their public image and the make-up of their collections. And finally, there are still some potential tensions between conservation and welfare which need to be resolved. These include the problem of surplus or unwanted animals generated by genetically managed programmes, and the use of interactive events between the animals and the public as a way of generating funding for conservation. These are briefly returned to in **Chapter 15**. So, there are clearly some challenges for zoos in the immediate future.

Summary

• The roles and priorities of zoos have changed substantially in the last 200 years, but most accredited zoos now cite conservation as their greatest priority.

• In the short term, captive management of breeding populations (*ex situ* conservation) is necessary for many species, with the aim of using them to supplement vulnerable wild populations, or to form new wild populations if they have already become extinct.

• The ways in which zoos should be involved in conservation are elaborated in two strategy documents, the *World Zoo and Aquarium Conservation Strategy* (WZACS) (WAZA 2005) and its predecessor, the *World Zoo Conservation Strategy* (WZCS) (IUDZG/CBSG 1993). Both the WZCS and the WZACS advocate an integrated approach to conservation both within and outside the zoo.

• The WZACS sees *in situ* conservation as the ultimate goal and many zoos are involved in this, either directly through field work or indirectly through activities such as fundraising.

• Some notable successes have been achieved in releasing zoo-born animals back into the wild, but this has not yet been a significant part of zoo conservation efforts.

Questions and topics for discussion

1. How good are zoos at conserving biodiversity?

2. How should zoos prioritize which species they keep?

3. Under what circumstances should zoos be permitted to keep and breed species that are not endangered and are not part of a recognized captive breeding programme?

4. 'If zoos did not exist, they would have to be invented.' To what extent, and why, do you agree with this statement?

5. How helpful is the distinction between *in situ* and *ex situ* conservation work by zoos? Can you suggest a more appropriate terminology?

Further reading

A comprehensive and critical assessment of the role of zoos in conservation is given in Fa *et al.*'s *Zoo Conservation Biology* (2011). Although published more than 20 years ago, a good book about the role of zoos in conservation is Colin Tudge's *Last Animals at the Zoo* (1992), which also gives a lot of information about captive breeding of endangered species. Another book that has stood the test of time, and which is still widely read and cited today, is Olney *et al.*'s *Creative Conservation: Interactive Management of Wild and Captive Animals* (1994). A recommended book for readers interested in the link between animal behaviour and conservation is Festa-Bianchet and Apollonio's *Animal Behaviour and Wildlife Conservation* (2003). For a discussion of what people working in the field of conservation think should be the role of zoos, Zimmermann *et al.*'s *Zoos in the 21st Century:*

Catalysts for Conservation? (2007) is not an easy read, but is very thought-provoking. Finally, there are two chapters in *Wild Mammals in Captivity* (Kleiman *et al.* 2010), which give information on reintroduction (Earnhardt 2010) and on how zoos can contribute to *in situ* conservation (Zimmermann 2010).

Websites and other resources

The *World Zoo and Aquarium Conservation Strategy*, published under the title *Building a Future for Wildlife* (WAZA 2005), is both accessible and readable, as is the equivalent strategy document for the aquarium community, *Turning the Tide* (WAZA 2009). These documents can be downloaded from the WAZA website (**http://www.waza.org**) and is a good starting point for further reading about how accredited zoos and aquariums are expected to be involved in the conservation of biodiversity.

Conservation activities often move very quickly and are not always reported in the scientific literature, so a good way of finding out more about the projects in which zoos are currently involved is to look at the websites of the individual zoos themselves, as well as those of the associations such as BIAZA, EAZA, AZA, and ZAA.

The IUCN website (**http://www.iucn.org**) features a considerable amount of information, including a searchable version of the Red List.

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.

http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Chapter 11
Health

Good zoos are concerned with both the physical and the psychological health of the animals in their care. Psychological health has already been considered in the chapter on welfare (**Chapter 7**), so this chapter will focus largely on the challenges of monitoring and maintaining physical health in zoo animals. There is, of course, considerable overlap between health and welfare, and signs of disease in captive animals (such as a high parasite load) are often used as measures of welfare. Not all disease will give rise to poor welfare, however; some minor health problems, such as benign fatty tumours, may not give rise to any pain or suffering.

Nutrition also plays an important role in the maintenance of good health. Nutritional diseases, such as metabolic bone disease and iron-storage disease (**haemochromatosis**), are mentioned briefly in this chapter; a more detailed account of the relationship between health and diet, along with other aspects of zoo animal nutrition, is provided in the next chapter (**Chapter 12**).

It would not be possible in a book of this size, let alone in a single chapter, to cover all aspects of zoo animal health in anything like sufficient detail to be of practical use to zoo staff. Instead, the aim of this chapter is to provide an overview of the main animal health care issues in zoos. The main topics that we will be considering in this chapter are as follows.

11.1 **What is 'good health'?**
11.2 **Guidelines and legislation on health of zoo animals**
11.3 **The role of zoo staff in zoo animal health care**
11.4 **Preventive medicine**
11.5 **Diseases of concern in zoo animals**
11.6 **The diagnosis and treatment of disease in zoo animals**

Short accounts of special topics in zoo animal health are included in boxes throughout this chapter. These include the challenges of dentistry for zoo animals and anaesthesia for giraffes, as well as a brief summary of how vaccines work.

11.1 What is 'good health'?

Assessing good health in a wild animal in captivity is not always straightforward. Signs of disease or even injury may not be outwardly obvious and an accurate picture of an animal's health may only be possible after **invasive procedures** such as **endoscopy** (**Fig. 11.1**) or blood testing for immune function (**Fig. 11.2**). Failure to reproduce can be due to underlying

Figure 11.1 Here, a vet is performing an endoscopy on a cheetah *Acinonyx jubatus* at the Cango Wildlife Ranch in South Africa, to try to determine the cause of a health problem. The diagnosis and treatment of health problems in large wild animals presents a number of challenges and, consequently, zoos place a strong emphasis on preventive medicine. (Photograph: Cango Wildlife Ranch)

health problems, but can also occur because of a lack of compatibility between individuals (see **Chapter 9**). Weight change can be a sign of disease (for example, in non-domestic felids, see Storms *et al.* (2003); in swift parrots *Lathamus discolor*, see Gartrell *et al.* (2003)), but can also occur for a variety of other reasons, such as a change in reproductive status or seasonal patterns of fat deposition (**Plate 11.1**).

Maintaining good health in zoo animals requires, as a minimum, routine monitoring of animals by knowledgeable members of staff who are familiar with the animals in their care. Keepers, and their managers, should have an understanding of species **life history traits** (such as age at sexual maturity, reproductive lifespan, etc.) and should maintain detailed current records of the animals in their care to identify any recurring health problems or other issues. All UK zoos must (by law) have access to qualified experienced veterinary support for the prompt treatment of sick or injured animals, together with facilities for the isolation and treatment of sick animals. Good **preventive medicine**,[1] including hygiene, pest control, **quarantine**, and vaccination (see **section 11.4**), is a very important part of zoo animal health care; for wild animals in captivity, it is nearly always easier to prevent disease from occurring in the first place than it is to treat it effectively later on.

Husbandry plays an important role in the maintenance of health, via the feeding of an appropriate diet and provision of appropriate housing, including heating and specialist lighting where necessary (see **Chapter 6**). In its broadest sense, husbandry also includes the management of human–animal interactions, such as visitor interactions with animals, to minimize the risk of injury and stress.

11.1.1 How can good health be assessed in zoo animals?

Even a small to medium-sized zoo may hold upwards of a thousand individual animals. The zoo keepers, who deal with the animals on their 'section' on a daily basis, are best placed to report possible health problems. Possible indicators of

---

[1] **Preventive** and **preventative medicine** are the same thing; both spellings are correct. 'Preventive' is the more usual spelling in the USA and in many veterinary textbooks, and appears to be gaining ground as the preferred spelling (in the UK, the BBC now uses 'preventive' rather than 'preventative' medicine). The contrasting term, once a disease has developed, is **curative medicine**.

Figure 11.2 Taking a sample of blood for testing from a wild animal in captivity will usually involve sedating or anaesthetizing the animal, as in the case of this zebra *Equus burchellii* at Singapore Zoo. Capture, restraint, and anaesthesia of a large wild animal poses risks both to the animal and to keepers and vets, so most zoos will not take blood samples routinely, but only when an appropriate opportunity presents itself (if, for example, an animal is being anaesthetized for other reasons). (Photograph: William Nai, Singapore Zoo)

an underlying health problem are summarized in **Table 11.1**, and include changes in behaviour (Dawkins 2003), body condition, gait, weight, or simply the (admittedly subjective) feeling that something is 'not quite right' (**Fig. 11.3**).

It is a problem to determine what is 'normal' because there are usually no hard and fast definitions of what is 'normal' for the species or individual animal. An understanding of what is 'normal' comes with experience, and applies as much to the behaviour of the animal as to its body weight and physiological or health parameters. It is also usually not practical to monitor the temperature, pulse, and respiration (TPR) of zoo animals on a regular basis. However, zoos can make use of other methods of monitoring health in their animals, such as **body**

Figure 11.3 Health problems in wild animals (both in zoos and in their natural habitat) are not always obvious. Spotting a possible health problem requires keepers to have a good knowledge of the animals in their care and sufficient experience to be able to judge when something is not quite right. An animal that has a hunched posture or is isolated from others in a social group may have an underlying health problem, as suggested by the behaviour of this dhole *Cuon alpinus*. (Photograph: Zoo Dresden)

External sign	Notes
Loss of appetite or refusal to drink	Reduced food or water intake by an individual animal can be difficult to monitor in group-housed species
Behaviour associated with ill health, such as coughing, fits, colic, staggering, isolation from group	To notice a change in behaviour, keepers must be familiar with the 'normal' behaviour of an animal
Changes in defecation or urination	Diarrhoea, cloudy urine, etc. can indicate a health problem (but might also result from a sudden change in diet)
Posture and gait	A sick animal may be hunched or unwilling to stand, or may show a change in gait
Appearance of skin, coat, and whole animal	Swollen areas of skin indicate inflammation; coats should be glossy not dull; areas of hair loss can indicate health problems such as mange or ringworm
Vomiting	Not all animals are capable of vomiting (e.g. equids cannot vomit)
Signs of pain	See **Chapter 7** for further information about the assessment of pain
Colour and appearance of mucous membranes	Mucous membranes (e.g. inside the mouth) should be pink; pallor can indicate anaemia and a bluish colour can indicate low levels of oxygen in the blood
Temperature, pulse, and respiration (TPR)	Rapid breathing or pulse and/or an elevated temperature (fever) can indicate ill health; however, normal body temperature is variable even between **homeothermic** species

Table 11.1 External indicators of possible health problems*

*For a comprehensive guide to parameters that can be assessed by visual inspection, see section 2.5 in the *Zoos Expert Committee Handbook* (Defra 2012b).

condition scoring (**Fig. 11.4** and **Box 11.1**) and **gait scoring**. Widely used by livestock farmers (e.g. Russel 1984), condition scoring can also be used for a variety of animals in zoos; gait scoring involves looking at the rate, direction, and range of movement of an animal, as well as the strength or force of its gait. Indicators that something may be awry could include a low-stepping gait, or an animal that is stumbling or wobbly on its feet.

11.1.2 Why can good health sometimes be compromised in zoo animals?

Animals in a zoo are protected from some of the health risks faced by wild animals by measures such as vaccination and the provision of an adequate diet. But all animals die eventually and ill health is, at some stage, an inevitable part of zoo animal life. Disease may be spread by contact with **conspecifics**, or with **free-ranging** species (exotic or native), or by **pests** such as rats and mice, or by keepers or visitors to the zoo. Animals may also be injured in fights with conspecifics, particularly after introduction into a new social group, or during mating. Just as for animals in the wild, complications can occur in female mammals and birds during parturition or egg-laying. Sometimes, trauma (that is, an injury or wound) can occur as a result of poor enclosure design (for example, an animal that

Score	1: Emaciated	2: Thin	3: Fair	4: Good	5: Heavy
Outline depictions					
Neck & shoulders	• Neck is narrow and angular (bony) • Nuchal ligament prominent • Prescapular groove deep and obvious • Shoulders are angular, bony	• Neck is flat and narrow • Nuchal ligament visible • Prescapular groove is obvious • Shoulders are flat and slightly bony	• Neck is rounded • Prescapular groove is slightly visible • Shoulders are flat.	• Neck is well muscled and rounded • Shoulders are rounded	• Neck is thick, well muscled, and rounded • Shoulders are well muscled and rounded
Scapula & ribs	• Scapula and ribs are very obvious	• Scapula and ribs are obvious	• Scapula and ribs visible	• Scapula is covered • Ribs are covered (skin folds)	• Scapula is covered • Ribs are well covered (skin folds)
Spine	• Groove along backbone is very obvious • Spinous processes are very prominent	• Deep groove along backbone obvious • Spinous processes are prominent	• Groove along backbone visible • Spinous processes are visible.	• Backbone is slightly angular • Spinous processes are slightly visible	• Backbone is rounded • Spinous processes are covered.
Rump & tail base	• Obvious depression in the rump • Pelvic bones are very prominent • Tail base is very thin and bony	• Rump is concave • Pelvic bones are prominent • Tail base is slightly bony	• Rump is slightly concave • Pelvic bones are visible • Tail base is narrow	• Rump is flattened • Pelvic bones are slightly visible • Tail base is rounded	• Rump is well rounded • Pelvic bones are covered • Tail base is rounded (bulging)
Abdomen	• Abdomen is tucked in • Flank folds are obvious	• Abdomen is tucked in • Flank folds are visible	• Abdomen is slightly tucked in • Flank folds are slightly visible.	• Abdomen is filled • Flank folds sometimes slightly visible	• Abdomen is distended and tant • No visible flank folds

Figure 11.4 Body condition scoring is a useful method of estimating the amount of fat that an animal has, as an indicator of general body condition and fitness. These kinds of diagrams have been used widely in livestock farming for many years, and more recently have been adopted by zoos for assessing body fat levels in captive animals. The diagram here shows body condition scoring for a black rhinoceros *Diceros bicornis*. (Reproduced with kind permission from Walt Disney Parks and Resorts: Animals, Science and Environment Line of Business)

Box 11.1 BODY CONDITION SCORING

Body condition scoring is a method of measuring the general body condition of an animal, as an indication of its nutritional and energetic state (Millar and Hickling 1990). Condition scoring has been used in livestock husbandry for some time, but can also be useful for the assessment of **fitness** in zoo animals. Body condition scoring can be determined by visual assessment, or by handling an animal. Russel (1984) describes a commonly used method of condition scoring in livestock, in which the stockperson feels along the spine of an animal and assesses the level of body fat covering the spine. The stockperson (or zookeeper) then records a score for the animal's condition. A score of 1, for example, describes an animal with a prominent spine and very little body fat; a score of 5 indicates a good layer of fat over the vertebrae, under which the joints on the spine can hardly be distinguished (**Fig. 11.4**).

Body condition scoring is subjective, but can be a useful measure if scores are recorded regularly by the same keeper or stockperson, for the same animal, over a period of time. The Defra website (**http://www.defra.gov.uk**) provides detailed and well-illustrated information about condition scoring in cattle; these methods can easily be adapted for other **bovids** and the general principle of condition scoring can be readily applied to a range of other **taxa**.

falls into a moat) or during capture and transport. Dietary problems can lead to poor health or even poisoning if inappropriate food items, such as toxic plants, are consumed.

There is very little in the peer-reviewed literature on health problems in zoo animals arising from poor enclosure design. We also know very little about the type and extent of harm caused to zoo animals by zoo visitors,[2] either intentionally or unintentionally; there is a need for data from systematic studies in this area of zoo animal health. But there are many anecdotal reports of health problems in zoo animals when litter or human foodstuffs have been ingested, either by accident or as a result of deliberate feeding (for example, soft drinks cans or beer bottles given to chimpanzees; penguins ingesting lollipop sticks or coins).

A particular problem for zoos that are involved in the breeding of rare or endangered species is that **genetic diversity** can be low in captive populations, leading to an increased risk of **inbreeding** and genetic abnormalities (this can also be true of some populations of animals in the wild). Genetic diseases in zoo animals are discussed in **section 11.5.2**.

11.2 Guidelines and legislation on the health of zoo animals

As has been pointed out already in this book, animals living in the wild are not free from pain, disease, stress, or hunger. Zoos cannot guarantee their animals a life free from disease or pain, nor can legislation ensure this, but zoos can, and should, monitor their animals effectively and ensure that any **clinical** or **pathological**[3] problems are treated promptly and appropriately.

11.2.1 UK legislation on zoo animal health and veterinary care

UK legislation governing the operation of zoos has already been considered in some detail in **Chapter 3**, so this section provides only a brief summary of legislation specific to zoo animal health. The Zoo Licensing Act 1981 does not have a great deal to say about animal health, other than to require zoos (as part of their conservation measures) to keep records '*of the health of the animals*'. The Act also stipulates that zoo inspections must cover the '*health, welfare and safety of the public and animals*', and that an experienced vet familiar with treating **exotic animals** must be appointed for special inspections (if these relate to animal health).

For zoos within the UK, section 3 of the Secretary of State's Standards of Modern Zoo Practice (SSSMZP) (Defra 2012a) (see **section 3.4.2**), entitled 'Provision of animal health care', sets out a number of recommendations relating to health care and veterinary facilities in zoos, covering, for example, routine observation of animals (see **Table 11.2**).

All zoos within the UK, regardless of size, are expected to maintain adequate on-site facilities for the examination and treatment of animals, including a dedicated veterinary treatment room (minimum requirements for veterinary facilities are set out in Appendix V of the SSSMZP) (**Fig. 11.5**). For UK aquariums and zoos that hold aquatic animals, the SSSMZP also sets out a requirement for the provision of on-site holding tanks, for the isolation of sick animals.

Zoo animal health: other UK legislation

Zoos must comply with specific animal health legislation, which, for zoos in the UK, can be at national or at EU level. For example, there is specific

---

[2] Heini Hediger, in his book *Wild Animals in Captivity* (1950), records a number of unpleasant instances of zoo visitors behaving badly, including putting pins into an apple before feeding it to an elephant. This shows, sadly, that there is nothing new about a small minority of zoo visitors causing harm to the animals.

[3] The root *patho-* means 'disease'—hence **pathology** is the study of disease and a **pathogen** is an agent that can cause disease. Pathogens can be bacteria, viruses, fungi, or other organisms, such as protozoan parasites. The prions that cause BSE and other spongiform encephalopathies are not micro-organisms; they are pathogenic proteins.

3.1	The condition, health and behaviour of all animals should be checked at least twice daily by the person or persons in direct charge of their care.
3.2	Any animals which give cause for concern must be thoroughly assessed as to whether they are unduly distressed, sick, or injured. Where necessary they must receive immediate attention and treatment.
3.3	A daily record must be kept by the person or persons in direct charge of the animals, indicating changes to the prescribed diet, health checks carried out, any unusual behaviour or activity or other problems, and remedial actions taken.

Table 11.2 Minimum requirements for monitoring animals in UK zoos*

*From the Secretary of State's Standards of Modern Zoo Practice (Defra 2012a).

EU legislation[4] on the monitoring of animals for **transmissible spongiform encephalopathies (TSEs)**, such as **bovine spongiform encephalopathy (BSE)**, and **chronic wasting disease (CWD)** (see **section 11.5.4** and **Fig. 11.6**). This requires, among other things, that zoos must test for TSEs in 'fallen stock' (that is, animals that have died) over two years of age. In practice, many zoos err on the side of caution, and will send **post-mortem** material from zoo bovids and felids for testing for TSEs even when they are not required to do so by law.

UK zoos are also legally required (as are farmers and other owners of animals) to report any cases of notifiable diseases in their animals (see **section 11.5.3**), under the terms of the Animal Health Act 2002 (this extended the powers of the Animal Health Act 1981). Appendix 1 to Chapter 5 of the *Zoos Expert Committee Handbook* (Defra 2012b) provides a comprehensive summary of the areas of UK legislation which govern veterinary work in zoos.
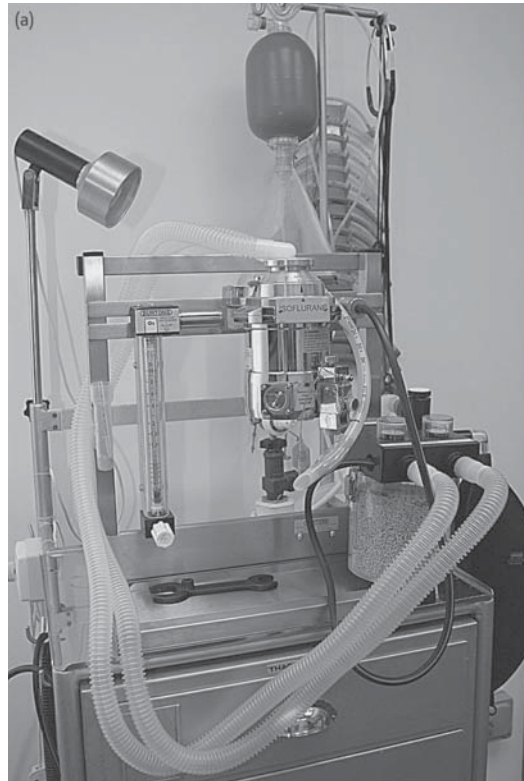
Figure 11.5 (a) Anaesthetic equipment in a zoo veterinary hospital; (b) anaesthetic equipment in use at another zoo, on a squirrel monkey *Saimiri sciureus*. There is a legal requirement for zoos within the UK to maintain on-site health care facilities for their animals, including a veterinary treatment room. (Photographs: (a) Paignton Zoo Environmental Park; (b) Mel Gage, Bristol Zoo Gardens)

[4] Within the EU member states, Regulation (EC) No. 999/2001 lays down rules for the prevention, control, and eradication of certain transmissible spongiform encephalopathies.

Figure 11.6 The greater kudu *Tragelaphus strepsiceros* is one of a number of bovid species kept in zoos that are susceptible to transmissible spongiform encephalopathies (TSEs), such as bovine spongiform encephalopathy or BSE ('mad cow disease'). In the UK, zoos are required by law to test for TSEs in animals over two years of age which have died. (Photograph: Liam Kite)

11.2.2 Legislation outside the UK on zoo animal health

Zoo animal health care: European legislation

As we saw in **Chapter 3**, all countries that are members of the EU are bound by the 1999 EC Zoos Directive.[5] This requires zoos to have '*a developed programme of preventive and curative veterinary care and nutrition*'.

The Balai Directive

The 1992 **Balai Directive**[6] has been discussed already in this book (see **section 3.3.2**). To recap briefly here, this Directive governs the transport of non-domestic animals between European countries, and also between EU and third-party countries, in relation to veterinary screening and

Figure 11.7 Moving zoo animals (e.g. as part of a captive management programme) is a complex business, and zoos must comply with a wide range of different legislation governing animal transport, animal health, and animal welfare. For example, EC Regulations on the transport of animals require veterinary screening of the animal prior to transport. Here, an okapi *Okapia johnstoni* is being loaded into a crate prior to being moved. (Photograph: Mel Gage, Bristol Zoo)

animal health (**Fig. 11.7**). 'Balai-approved' zoos are required to meet certain requirements, such as the production of a health surveillance plan (which must be reviewed annually) and confirmation that the zoo has enrolled the services of an **approved vet (AV)**.

Annex A to the Balai Directive lists a number of infectious diseases, but these are largely diseases that do not normally occur in the UK (for

---

[5] EC Directive 1999/22/EC relating to the keeping of wild animals in zoos.
[6] Council Directive 92/65/EEC of 13 July 1992 laying down animal health requirements governing

trade in and imports into the Community of animals, semen, ova, and embryos not subject to animal health requirements laid down in specific Community rules referred to in Annex A (I) to Directive 90/425/EEC.

example, swine fever, rabies, and anthrax). It is also worth noting that the diseases listed in Annex A of the Balai Directive are diseases of mammals and birds; the Directive does not cover the diseases of other taxa (with the exception of bees).

Zoo animal health care: legislation outside the European Union

Outside Europe, the picture is mixed. In the USA, zoo animal health falls largely under the banner of the Animal Welfare Act of 1966 (AWA). The AWA covers aspects of veterinary treatment of zoo animals, as well as animal purchase, transportation, housing, handling, and husbandry (Vehrs 1996). As Spelman (1999) points out, the AWA also includes a requirement that licensed animal facilities (including zoos) maintain a pest control programme. As noted in **Chapter 3**, the AWA regulations apply only to selected mammalian species and not to other taxa; farm animals, rats and mice, and most common companion animals are excluded from the provisions of the Act (Vehrs 1996).

In Australia, the six state and two territory governments have considerable responsibility for legislation relating to animal health and animal welfare. Animal Health Australia (AHA) is a not-for-profit public company established by the national, state, and territory governments to coordinate animal-health-related activities, such as disease surveillance; the AHA website contains much useful information on animal health in general, including the health of zoo animals.

11.2.3 Guidelines and other sources of information about zoo animal health

Husbandry guidelines produced by **European Endangered Species Programmes (EEPs)** and (in the USA) **Species Survival Plans (SSPs)** usually include a section on health care. Zoo vets also have access to the conferences and conference proceedings of regional organizations such as the European Association of Zoo and Wildlife Veterinarians (EAZWV). The EAZWV was established in 1996 (**http://www.eazwv.org**); there is also the American Association of Zoo Veterinarians

(AAZV), the website of which (**http://www.aazv.org**) contains much useful information. Meehan (2012) provides a useful summary of the AAZV guidelines for zoo animal medicine and hospitals in zoos and aquariums. The EAZWV and AAZV are the joint publishers of an important journal for zoo vets: the *Journal of Zoo and Wildlife Medicine*, and indeed all these organizations publish information regularly, in the form of guidelines, newsletters, journals, and proceedings from meetings. Zoo organizations such as EAZA, AZA, and ZAA (formerly ARAZPA) also set their own standards for veterinary care for member collections.

11.3 The role of zoo staff in zoo animal health care

Animal health care responsibilities in zoos are shared between zoo veterinary staff, keepers, and other staff, such as zoo animal nutritionists (**Fig. 11.8**). The role of a zoo vet can be very broad and demands knowledge of a wide range of topics, including husbandry and nutrition, legislation, computerized record-keeping, statistics, and conservation genetics. The same is true for most zookeepers, and, within a zoo, veterinary staff and keepers will be responsible for most, if not all, of the following areas of animal health care provision, depending on the size of the zoo and the range of its activities:

- animal identification, including sexing animals;
- preventive medicine, including biosecurity;
- the diagnosis of ill health;
- diet and nutrition;
- the treatment of sick or injured animals, including restraint and anaesthesia;
- post-mortem examinations and carcass disposal;
- reproductive management—that is, support for population management and **captive management programmes**;
- the training of other veterinarians, keepers, students, etc.;

Figure 11.8 Animal health care responsibilities in a zoo are shared between keepers, veterinary staff, and support staff. Here, a team of keepers and veterinary staff at Werribee Open Range Zoo, near Melbourne in Australia, are working together to examine and treat a sedated Przewalski's horse *Equus ferus przewalskii*. (Photograph: Chris Stevens, Werribee Open Range Zoo)

- health checks (and paperwork) in relation to the transportation of animals;

- the recapture of escaped animals;

- support for conservation initiatives and field-work (including *in situ* work);

- human health and safety (for example, in relation to zoonotic diseases, or the use of firearms, or dangerous drugs); general issues relating to the health and safety of zoo staff and visitors are considered in more detail in **Chapter 6**).

These topics are explored in more detail in the following sections of this chapter. Of this list, the diagnosis of health problems in zoo animals presents perhaps the greatest challenge and is the main skill required of a good zoo vet.

There are three main areas in which zoo animal health care can differ from that of farm or companion animals (although there is also considerable overlap in the skills required). Firstly, preventive medicine is of great importance in zoos; treating sick or injured wild animals is particularly difficult and costly, so it is much better to try to prevent them becoming ill in the first place. This is also true, to a certain extent, in livestock practice, but differs somewhat from companion animal practice, in relation to which (other than routine vaccinations, worming, and treatment for fleas) vets may only see an animal once their owner has realized that their pet is ill or injured.

Secondly, a zoo vet will work with keepers as part of a team for capture, restraint, and treatment of animals, and may train keepers to perform minor veterinary procedures such as **venepuncture**. This is not usually the case in companion animal medicine (but may be the case for livestock vets and stockpersons).

Finally, zoos may only know for certain what was wrong with an animal once it has died, and the zoo has been able to carry out pathological tests and a post-mortem examination.

11.3.1 Zoo veterinary staff

A zoo vet may well encounter rare diseases and health problems that a farm animal vet or domestic animal vet has never seen, although many of the challenges of maintaining good health in zoo animals are broadly similar to the challenges of providing health care for other animals kept in captivity (for example, farm animals). Zoo vets are also more likely than livestock or companion animal vets to see an animal from 'cradle to grave', and even beyond this; a zoo vet may well be involved before and after an animal's life (**Fig. 11.9**).

Within the UK, few zoos have full-time veterinary staff on the premises. Smaller zoos and wildlife parks are likely to use the services of an external veterinary practice within which there is some expertise in the treatment of exotic animals. However, a larger zoo may have an animal health team comprising one or more full- or part-time veterinary surgeons, one or more veterinary nurses, and, sometimes, an in-house pathologist[7] and/or nutritionist as well. Saint Louis Zoo in Missouri, USA, for example, has a veterinary hospital complex that incorporates six laboratories, a radiology suite, and a surgery suite, as well as a quarantine wing. The veterinary staff team at Saint Louis includes a full-time nutritionist, and an endocrinology team that works

Figure 11.9 A young crocodilian hatching from its egg at Cango Wildlife Ranch in South Africa. Zoo vets are involved in an animal's life not only from 'cradle to grave', but often from before an animal's birth to after its death. Pre-birth work may include the monitoring of the reproductive status of the mother; after an animal's death, the veterinary team is responsible for carrying out a post-mortem examination. (Photograph: Cango Wildlife Ranch)

within Saint Louis Zoo and also offers support to other, smaller zoos.

11.3.2 Veterinary involvement in captive management programmes

Zoo vets may be involved in captive management initiatives at both national and international levels, usually via organizations such as the British and Irish Association of Zoos and Aquariums (BIAZA), EAZA, AZA, ZAA, and the World Association of Zoos and Aquariums (WAZA), etc. (see **Chapter 3**). Vets may provide advice to taxon working groups (TWGs) and **taxon advisory groups (TAGs)**, and to **studbook** managers or those involved in programmes such as the European Endangered Species Programmes (EEPs) or, in the USA, Species Survival Programmes (SSPs).

An example of how veterinary support can contribute to the success of a captive management programme is provided by Seebeck and Booth (1996), who describe the extent of veterinary

---

[7] The work of a **pathologist** involves carrying out diagnostic **necropsies** to determine the cause of

disease. Diagnostic tests can be performed on animal tissues, blood, faecal matter, urine, or saliva.

Figure 11.10 Veterinarians have played an important role in conservation efforts to protect the critically endangered eastern barred bandicoot *Perameles gunnii*, a rabbit-sized nocturnal marsupial found in Tasmania and western Victoria, Australia. Veterinary involvement in captive breeding and reintroduction attempts for this species has included investigation of parasitism as a cause of death or poor health in these animals. (Photograph: J.J. Harrison/CC-BY-SA)

involvement in the recovery programme for the critically endangered eastern barred bandicoot *Perameles gunnii* in Australia (**Fig. 11.10**)

11.3.3 Veterinary inspection processes for zoo animal transportation

Vets are involved not only with the health care of animals living in a zoo, but also with the arrangements for the transport of animals between zoos (for example, as part of a breeding programme). In the UK, for example, an animal that is being exported overseas must have an export licence granted by Defra and this licence must be signed by the local Defra Veterinary Inspector on the day of departure of the animal. Even if an animal is from, and is destined for, a Balai-approved zoo, veterinary approval and signature are still required (see **section 11.2.2** and **Chapter 3**). Other documents that may be required for transportation and which need veterinary input include any medical notes.

Zoo vets may also be involved in the capture of animals for transport, as, of course, are keepers (**Fig. 11.11**).

Figure 11.11 As in **Fig. 11.8**, this photograph shows the team work necessary for successful animal health care in zoos. Here, keepers and veterinary staff at Colchester Zoo are working together to move an anaesthetized tiger (the tail of the animal is just visible on the far right) from its enclosure to the veterinary hospital for treatment. (Photograph: Colchester Zoo)

11.3.4 Veterinary support for wildlife management outside the zoo

Increasingly, zoo vets (and other zoo staff) are involved in *in situ* wildlife management and conservation projects.[8] A US zoo pathologist,

[8] The Wildlife Conservation Society (WCS), based in New York, provides further examples of the role that vets (not only from zoos) can play in wildlife management and conservation, as well as much useful information for field vets (see the 'Resources and Technical Pages' of the 'Wildlife Health' section of the WCS website (**http://www.wcs.org**)).

Figure 11.12 Common dormice *Muscardinus avellanarius* are bred in captivity at several zoos within the UK as part of wider conservation programmes for their reintroduction back into selected sites in the wild. Before release into the wild, these animals are screened for diseases such as tuberculosis and for the presence of gut parasites. This photograph shows an anaesthetized dormouse being weighed as part of routine health monitoring. (Photograph: Paignton Zoo Environmental Park)

for example, was among the team of investigators who first discovered the link between the rapid decline in numbers of vultures in Asia and the widespread use of the non-steroidal anti-inflammatory drug (NSAID) diclofenac in domestic livestock (Oaks *et al.* 2004). Keepers and vets from a number of zoos worldwide have since been involved in attempts to reduce the threat posed by diclofenac to critically endangered Asian vulture species by providing both facilities and captive-bred birds of closely related species for testing of an alternative and less damaging NSAID, meloxicam (Swan *et al.* 2006). In the UK, vets from a number of zoos are involved in carrying out health tests on captive-bred animals prior to their release back into the wild. Common dormice *Muscardinus avellanarius*, for example, are routinely tested for tuberculosis (TB) prior to release (**Fig. 11.12**).

11.4 Preventive medicine

Preventive medicine and care play a very important role in zoos, because successful diagnosis and treatment of disease in wild animals can be particularly challenging. All zoos, from the smallest to the largest, will be involved at some stage in

one or more areas of preventive medicine, ranging from basic health checks to quarantine procedures; vaccination; foot, beak, and dental care, and post-mortem examinations. Much zoo husbandry is also part of preventive medicine; provision of an appropriate diet, hygiene, pest and parasite control, and enclosure design and management are every bit as important in preventing disease as vaccination or regular veterinary checks of animals.

All these measures can be grouped under the general heading of biosecurity. This can be as simple as requiring keepers to change into clean uniforms and footwear when they arrive on site, to reduce the risk of transmitting infectious diseases into the zoo. (The Defra website features further information about biosecurity measures; although aimed at livestock farmers, much of this information is also relevant for zoos.)

11.4.1 Health examinations

Requirements for the routine monitoring of the health of zoo animals have been discussed already in this chapter (see **Table 11.2**), but one area of zoo animal health screening that has not yet been considered is dental health. **Box 11.2** provides a brief account of some aspects of dentistry for zoo animals.

11.4.2 Quarantine

Preventive medicine often starts with the careful selection of new animals and a period of quarantine or isolation. Quarantine periods vary considerably, depending both on the species and its country of origin, and on the country it is going to. For example, in Europe it depends on whether or not the animal is being imported into a Balai-approved zoo from another Balai-approved institution (see **section 3.3.2**). For example, for non-Balai-approved zoos within the UK, equids are usually quarantined for a minimum of 30 days on arrival, whereas primates are usually kept in quarantine for between 60 and 90 days, largely because of the time lapse between TB

Box 11.2 DENTISTRY FOR ZOO ANIMALS

Tooth care poses particular problems in zoo animals, not only because of the physical demands and potential dangers of working with large wild animals, but also because of the very wide variety of tooth sizes and structures that a wild animal dental surgeon may be required to treat, from chimpanzee molars, to elephant or walrus tusks (Glatt *et al*. 2008). For example, Wiggs and Lobprise (1997) suggest that 3–6-inch drill bits may be needed for canal work on the canines of large **Carnivores** such as tigers; small sledgehammers and industrial power drills may be necessary for **pachyderm** dentistry. In zoos, dentistry is often a surgical procedure. For example, cheek tooth (premolar and molar) removal in large animals may have to be by means of a **buccotomy**, in which an incision is made in the face to access a diseased tooth from the outside, rather than via intra-oral extraction as would be the case in human patients.

Diagnosis of dental problems in zoo animals is not easy, unless animals have been trained to open their mouths for inspection. Signs of possible tooth problems include weight loss, a refusal to drink cold water, and the animal dropping food from its mouth or selecting only soft items of food. The mouth cavity may also bleed or smell offensive. Because routine oral inspection of wild animals in captivity is difficult, a full

Figure 11.13 The tusks of an elephant are extended teeth (incisors). Dental treatment for elephants in captivity is a major undertaking, as shown in these photographs from Colchester Zoo of an operation (a) on the tusk of Jambo, one of the elephants at the zoo. The successfully treated tusk can be seen more clearly in photograph (b). (Photographs: Colchester Zoo)

dental check-up is usually carried out whenever a zoo animal is anaesthetized for any reason (Wiggs and Lobprise 1997) (**Fig. 11.13**).

Braswell (1991) provides a short summary of some of the main problems in exotic animal dentistry, such as tusk and molar problems in elephants, and an oral disease known as 'lumpy jaw', which is relatively common in captive **macropods** such as kangaroos and wallabies (see also Canfield and Cunningham 1993).

infection and the development of a positive skin test. In the USA, the AZA recommends a minimum of 30 days quarantine for fish; the National Aquarium in Baltimore (and Washington, DC) sets a minimum of 90 days (Hadfield 2012).

In the UK, rabies legislation was amended in 2011, with the Non-Commercial Movement of Pet Animals Order 2011 coming into force from 1 January 2012.[9] This reduces the rabies quarantine period for rabies-susceptible mammals from six to four months, to bring the UK into line with slightly less stringent EU rabies requirements set out in Regulation (EC) No 998/2003. Further details about current UK rabies quarantine requirements are available from the Defra website.

The aim of quarantine is not simply to prevent the transmission of disease[10] from newly arrived animals to existing animals (or staff) in the zoo. Quarantine provides a period of time during which zoo staff can assess baseline health

---

[9] The full title of the UK Rabies Order is The Rabies (Importation of Dogs, Cats and Other Mammals) Order 1974.

[10] The transmission of disease can be 'vertical' (e.g. from mother to offspring, typically during gestation) or 'horizontal' (e.g. from one animal to another animal in the same, or a nearby, enclosure).

parameters, and also appetite and behaviour. Animals that have been moved from one location to another are likely to have experienced stress as a result of transportation; this can trigger the presentation of **clinical signs** for any subclinical disease, making any health problems easier to detect. A period of time in quarantine also allows the animal to recover from transportation, and to adapt to its new surroundings and to a new husbandry regime, before any potentially stressful introduction into a new social group or enclosure.

For further information about quarantine for zoo animals, Hinshaw *et al*. (1996) provide a useful summary, although this source is now rather dated. Hadfield (2012) considers issues relating to quarantine of fish and aquatic invertebrates.

11.4.3 Vaccination

Vaccines are available for use by zoo vets, but there are almost no commercial vaccines (as yet) that have been developed specifically with zoo animals in mind. This is one of the reasons why vaccination is less widely used in zoos than might be expected. Where zoo vets do vaccinate their animals, they must 'make do' with vaccines developed originally for farm or companion animals, and must extrapolate dosage information from data for domestic animals. They can make this procedure more accurate by monitoring the **serological response** of an animal after vaccination. **Box 11.3** provides a brief account of how vaccines work and considers the risks to wild animals of using 'live', rather than inactivated, vaccines.

Some vaccines can be given orally, but most animal vaccines are administered via subcutaneous (below the skin) or intramuscular injection, which usually requires the capture and restraint of the animal (**Plate 11.2**). Before vaccination takes place, zoo vets must weigh up whether the risk of vaccination (including capture and restraint) is greater than the risk of the animal contracting the disease. This will depend on the severity of the disease and the availability of other means of disease control. For any vaccination

programme to be safe and effective, vets need to be able to determine whether or not the vaccination has worked (for example, by monitoring the serological response of the animal) and to know how long a period of protection against disease the vaccination will provide.

Some of the more widely used vaccines in zoos are those against rabies (but not within the UK) and canine distemper virus (CDV) (but note the risks described in **Box 11.3** associated with the use of modified live CDV vaccines for some species), polio, tetanus, and measles vaccines for the great apes, and tetanus vaccines for equids and tapirs. Where equine encephalitis is prevalent, zoo equids are also often vaccinated against this disease. Hinshaw *et al.* (1996) provide further general information about vaccination for zoo mammals; Lamberski (2012) provides a review of vaccination recommendations for zoo Carnivores.

11.4.4 Hygiene (sanitation) and enclosure management

Achieving a high standard of hygiene in zoo enclosures should be based on good practice (such as regular 'poo picking'), with the use of disinfectants only as a last resort. Nevertheless, a wide range of disinfectants and commercial cleaning substances are used in zoos, but there is surprisingly little information available in either textbooks or the peer-reviewed literature about their effectiveness in killing pathogens, or about any possible risks associated with disinfectant use in the zoo environment.

Captive felids appear to be susceptible to poisoning from incorrect use of phenolic disinfectants (Hinshaw *et al*. 1996) and there is anecdotal evidence of toxicity from improper use of bleach (sodium hypochlorite) to clean enclosures. Most zookeepers rely on manufacturer's literature for information about dilution rates and application methods for disinfectants, and such data that are available tend to be based on farm, rather than zoo, usage.

In the UK, veterinary disinfectants for the control of notifiable diseases are placed on an

Box 11.3 HOW DO VACCINES WORK?

Vaccination makes use of a substance called an antigen, which is derived from the pathogen (infective agent). This stimulates the immune system of the vaccinated animal to respond, so that it is resistant to natural infection by the pathogen. Vaccination, if effective, protects against disease, but not always against infection (in other words, animals may still be infected with the pathogen after vaccination, even if they do not develop the full-blown disease).

There are two main categories of vaccine: live and killed. Live vaccines contain an attenuated or changed version of the pathogen that is less harmful than the natural version of the pathogen, but still triggers an immune response in the vaccinated animal (in this context, you may sometimes see the abbreviation ML for 'modified live', or MLV for 'modified live vaccine'). The use of live vaccines, however, can lead to problems such as abortion in mammals and may sometimes trigger the disease that the vaccine

is intended to prevent. This has happened in captive grey foxes *Urocyon cinereoargenteus*, where animals have died of vaccine-induced canine distemper (Halbrooks *et al*. 1981). Other non-domestic species in which vaccine-induced canine distemper has been reported include the African wild dog *Lycaon pictus* (McCormick 1983), the red panda *Ailurus fulgens* (Bush *et al*. 1976), and the black-footed ferret *Mustela nigripes* (Pearson 1977). Lamberski (2012) provides an overview of current vaccination recommendations for Carnivores (**Plate 11.2**).

Killed vaccines are less risky (and are also more stable in storage), but can also be less effective; the immunity they induce may be short-lived, necessitating booster vaccination at regular intervals. The disadvantages of traditional vaccines have led to the development in more recent years of what are referred to as 'third-generation'[11] vaccines, manufactured using biotechnology such as recombinant DNA or protein engineering.

---

approved list by Defra once they have passed laboratory tests. This listing process operates under the Diseases of Animals (Disinfectant Approvals) Order 1978. The current approved list is available online from the Defra website, together with a separate list of manufacturers and distributors of approved disinfectants.

Some methods of cleaning enclosures can increase, rather than decrease, the likelihood of the spread of disease (**Fig. 11.14**). Power hoses, for example, can spray a fine mist of water and faecal material over a wide area. The SSSMZP (Defra 2012a) specifically state that '*Health risks posed by the use of power hoses on animal waste must be minimized*'. Over-wetting of concrete floors can also be a contributory factor in the development of foot problems in some species, particularly elephants.

11.4.5 Pest control

A pest species may compete with the zoo animals for resources such as food or nest boxes, or may transmit disease. Animals regarded as pests in zoos include species such as cockroaches, pigeons, seagulls, herons, snakes, opossums, raccoons, and rodents such as rats and mice, which can all be **vectors** of disease. In North America, for example, cockroaches can transmit *Sarcocystis* (a **protozoan** parasite that can cause disease in birds such as **psittacines**) from opossum faeces (Lamberski 2003). Rodents can transmit diseases such as Lyme disease, via the tick vector *Ixodes scapularis*, to captive deer (Williams *et al*. 2002) and leptospirosis to primates, and can contaminate foodstuffs with *Salmonella* bacteria. Mice and rats are also intermediate hosts for parasites

---

[11] First-generation vaccines are those manufactured using whole organisms, such as the polio virus used in the polio vaccine; second-generation vaccines use just part of the virus, such as a surface antigen.

Figure 11.14 It is tempting to think that thorough power-hosing of an enclosure must be beneficial and will result in high standards of hygiene, but, in fact, the opposite can be true and the use of power hoses can spray faecal matter and other waste over a wide area. Good old-fashioned methods of enclosure cleaning (with a broom, or a shovel and wheelbarrow) are often better in terms of reducing the risk of disease. (Photograph: Sheila Pankhurst)

such as *Toxoplasma gondii*. At Baltimore Zoo, retrospective analysis of **mortality** in black-tailed prairie dogs *Cynomys ludovicianus* showed that 24 per cent of animals examined post-mortem had hepatic capillariasis caused by the parasitic nematode *Calodium hepaticum* (Landolfi *et al.* 2003). The authors of this study suggest that wild rats in the zoo may have acted as a reservoir for the disease.

Rodents, such as rats, are not only vectors of disease, but may be direct predators of eggs and nestlings of captive birds, as can snakes, raccoons, and opossums in North American zoos

(Lamberski 2003). Free-ranging birds can also spread diseases, such as chlamydiosis and salmonellosis, usually via faecal contamination of perches and food bowls. Effective pest control depends on enclosure integrity and design (preventing rats and mice from gaining access to exhibits, particularly to feeding areas), active pest control measures, and good hygiene in food preparation areas (see Spelman (1999) for a useful review of pest control in zoos, and Langan (2012), for an overview of **integrated pest management**[12] in zoos). The provision of **scatter feeds**, as part of **enrichment** for captive animals, is likely to

[12] Integrated pest management is an approach which aims to use the safest methods to control pest populations, starting with monitoring to determine whether control measures are needed. This approach considers the ecology of the pest species, and the likely impact of control measures on the pests, and on the animals and people in the zoo.

increase food accessibility to wild rodents (other possible health impacts of enrichment are considered further in **section 8.6**). The use of poisoned bait to control rodents poses the risk of potential ingestion by a non-target species, although careful location of bait and the use of bait traps can help to minimize this risk. Lamberski (2003) suggests a range of pest control measures for aviary birds, including placing food and water pans off the ground, the use of fine mesh along the bottom of aviaries to exclude snakes, rats, and other small mammals, and the use of electric wire to deter free-ranging mammals and birds from entering the aviary.

Zoos also face an ethical dilemma in relation to the control of rodent populations: the use of slow-acting anticoagulant rodenticides is regarded as an inhumane form of pest control (Mason and Littin 2003). The use of such rodenticides sits uncomfortably with public statements by zoos of concern about animal welfare. Snaptraps and electrocution devices, if used properly, kill rodents instantaneously and humanely, but some zoos now use **biological control** measures for pests. At the Burgers' Zoo in Arnhem in the Netherlands, for example, biological control methods are employed in the Bush rainforest exhibit (Veltman and van der Zanden 2000). Bauert *et al.* (2007) examine methods of pest control in their review of the first three years of operation of the Masoala rainforest exhibit in Zurich Zoo.

11.4.6 Parasite control

The control of parasites is a very important part of preventive medicine in zoos; many parasites, such as the ascarid worms of carnivores, are hard to eradicate once they are established in a captive population and can cause chronic health problems (Hinshaw *et al.* 1996). Parasites can be grouped into two categories:

- **ectoparasites**[13], which live on the body surface of the host animal;
- **endoparasites**, which live inside the gastrointestinal tract or the body tissues of the host.

The main ectoparasites are flies, lice, mites, fleas, and ticks. Some are protozoans, such as *Ichthyophthirius multifiliis*, which causes white spot disease in fish; this can be a problem in freshwater aquariums. Not all ectoparasites will be visible to the naked eye; some will require microscopic examination for identification.

Of perhaps greater concern are endoparasites, which can cause serious health problems and even fatalities. The majority of endoparasites are parasitic worms, or **helminths**, and protozoans. Some of the helminth genera which zoo vets commonly have to deal with are *Trichuris*, *Syngamus* (gapeworm), and *Ascaridia*. Protozoan parasites of concern include *Toxoplasma gondii* and *Coccidia*.

Trichuris trichiura, for example, is a commonly occurring helminth species often called the whipworm. It is a major zoonosis, and around a quarter of the world's human population is thought to be infected with this parasite. Light infections are often asymptomatic, but uncontrolled infections can result in anaemia and stunted growth.

The presence of helminths in the gut of zoo animals can be diagnosed by examining the animal's faeces for eggs shed by the worm or worms. There are numerous different methods for both detecting and quantifying parasite eggs in faecal matter, but no single method that reliably detects the eggs of all types of parasite. **Box 11.4** provides details of a commonly used protocol, the McMaster flotation technique, for assessing gastrointestinal worm burden by measuring faecal egg counts. This should be used alongside other methods of measuring parasite burden, such as sedimentation or filtration protocols, or a pasture larvae count.[14] The method chosen will depend on what is being looked for.

---

[13] **Ectoparasites** and **exoparasites** are the same thing—both spellings are correct

[14] The infective stage of many helminths is a larval stage that exists outside the host animal on grassland used for grazing by ungulates; these larvae can be detected using pasture larvae counts, in which a specific quantity of grass is cut and rinsed and the rinsing water poured through a series of fine mesh sieves to extract larvae of different sizes.

Box 11.4   THE McMASTER FLOTATION TECHNIQUE FOR MEASURING PARASITE BURDEN

The eggs of parasitic worms in the gut are shed with the faeces of the host animal, and can be counted and identified under the microscope (**Fig. 11.15a**). The result gives an estimation of the number of eggs per gram (epg) of faeces. This, in turn, can be used as an estimation of the degree of infestation of an individual animal, or a group of animals. Egg counts give information about both the prevalence of infection (that is, how many animals are infected in a group or population) and the intensity of infection (that is, how severe or heavy the parasite load is in infected animals). However, individually identified faecal samples are required for determining prevalence of infection, and these can be difficult to obtain for group-housed animals. More commonly, faecal samples will be collected from the group of animals, and these can only provide information about the intensity of infection within the group.

A commonly used method of measuring epg in faeces is to use a special chambered slide, called a 'McMaster slide' (**Fig. 11.15b**), to facilitate counting eggs suspended in a known quantity of a salt solution (because the eggs float to the surface of the solution, this method is also sometimes called a 'flotation technique'). The following protocol is a brief outline of how to carry out a faecal egg count using a McMaster slide (there are other similar but slightly different protocols; see for example **http://www.sheepandgoat.com/ACSRPC/Resources/fec.html**). For further information, see a good general textbook on practical or diagnostic parasitology. If you can get hold of a copy, MAFF's *Manual of Veterinary Parasitological Techniques* (1986) is a useful source; Garcia (1999) provides a review of the advantages and disadvantages of flotation methods versus other techniques for measuring parasite egg burden.

(a)

Figure 11.15 (a) Examining a faecal sample under the microscope for the presence of the eggs of gastrointestinal parasites. Laboratory work is an essential part of health care in zoos; samples may be sent out to specialist laboratories, but many larger zoos have their own laboratory facilities. (b) A McMaster slide, commonly used to facilitate counting parasite eggs in suspension in a solution. (Photographs: (a) Paignton Zoo Environmental Park; (b) Hawksley (Medical and Laboratory Equipment))

(b)
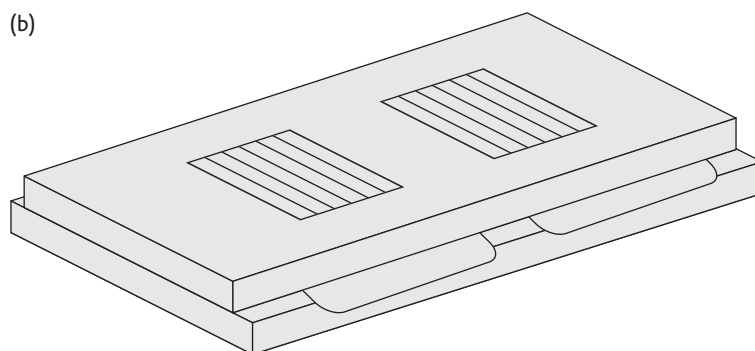
Disposable latex gloves should be worn for this procedure and all normal hygiene precautions for handling faecal matter observed.

Stage one: the collection of faecal samples
Faecal samples should be collected as soon as possible after emission. Early morning is often a good time to collect faeces. Faecal pellets should be collected into a sterile plastic container, which is then marked with the ID of the animal (if known) and the time, date, and place of collection. Samples can be kept in a fridge for up to 48 hours before analysis. Longer storage is not recommended, because the eggs can hatch; this can lead to a distorted count. Samples should not normally be frozen, because some types of egg may rupture and this will prevent identification.

Stage two: preparation of samples
- Place approximately 20 g of faecal matter (this is roughly ten large rabbit pellets, or a level tablespoon of other faeces) into a dish.
- Break/mash the sample up with a metal fork to mix the faecal pellets. This is because parasite eggs are often shed unevenly and one faecal pellet may contain many eggs, while another contains none; mashing several pellets together gives a more accurate overall egg count.
- Place 3 g of faecal matter (a level teaspoon) into a plastic tea strainer (aperture of mesh approx. 0.15–0.25 mm).

- Measure out 45 ml of saturated salt solution (370 g of NaCl dissolved in 1 litre of hot water) and pour this slowly over the faecal matter, mashing and pushing the sample through the strainer with a small spoon. Collect the filtrate in a dish or bowl.

Stage three: carrying out an egg count using a McMaster slide
- Using a Pasteur pipette, fill both chambers of a McMaster slide with the suspension.
- Wait for 60 seconds to allow the worm eggs to float to the surface of the chambers.
- Using a compound microscope (×10, ×40, ×100), carry out a count of all visible intact worm eggs between the marked areas on the two slide chambers.
- The number of eggs per gram of faecal matter (epg) is then obtained by multiplying the total number of eggs found in the two squares by 50 (for example, if ten eggs in total are counted, the epg is 500—that is, 500 eggs per gram of faecal matter).
- Egg counts can vary from zero to over 5,000 epg in a highly infected animal.

Stage four: egg identification
Using an appropriate guide, identify the eggs observed to genus or family level (where possible). Zajac and Conboy (2012) is an excellent and well-illustrated text.

Not all endoparasites inhabit the gut; parasitic worms and flukes can be present in organs such as the heart, lungs, and liver, and detecting their presence in a live animal may require invasive testing, such as taking a tissue sample.

Part of good husbandry in zoos is managing animals in such a way as to minimize the risk of infection with parasites, or to prevent the parasite completing its life cycle (this is a case of 'know thine enemy', or at least knowing something about its life cycle). Helminths can also be treated using **anthelmintic drugs**[15], which either destroy the worms on contact or paralyse them.

Zoos can administer anthelmintic drugs in a number of ways, such as topically, or in the food stuff given to animals, or in the form of an orally

---

[15] **Anthelmintic drugs** (the spelling **antihelmintic** is also correct) are drugs used to treat animals infected with parasitic gut worms, such as roundworms. Commonly used anthelmintic drugs in zoos include ivermectin (in branded drugs such as Oramec®, Ivomec®, and Acarexx®) and fenbendazole (in branded drugs such as Panacur®). Ivermectin is also effective against some ectoparasites, but is not effective against tapeworms or flukes.

Figure 11.16 Some zoo animals can be trained to accept oral administration of medicine, without the need for anaesthetizing or 'knocking out' the animal. This photograph shows a drug dose being administered to a lion-tailed macaque *Macaca silenus* at Ramat Gan Zoo in Israel. (Photograph: Tibor Jäger, Zoological Center, Tel Aviv)

administered drench that can be syringed into the mouth of an animal (**Fig. 11.16**). One of the problems associated with the use of anthelmintic drugs is that parasites can become resistant to treatment after repeated use; a secondary problem is that anthelmintics available to zoo vets have usually been tested and approved for use in livestock rather than wild animals in zoos (as we have already seen, this is also the case for vaccines).

A further problem faced by zoo vets and keepers when administering anthelmintic drugs is that of ensuring that every individual animal in socially (group) housed animals receives an adequate dose of the drug. In a long-term study of *Trichuris trichiura* infection in zoo-housed Abyssinian colobus *Colobus guereza kikuyuensis*, Melfi and Poyser (2007) found that individual administration of anthelmintic drugs to the colobus

(rather than social drug delivery via communally available food) resulted in a significant decrease in mean egg counts.

11.4.7 Foot care

Foot care is an important part of preventive medicine in zoos, particularly for **ungulates**.

Mammals

Hoof overgrowth is a common problem in species ranging from zebras and giraffes (**Fig. 11.17**) to rhinoceroses and elephants, and is often associated with unsuitable enclosure surfaces, genetic factors, and also copper deficiency. The hooves of ungulates are produced from a part of the foot called the corium and grow continuously throughout the animal's life. Normally, hoof

Figure 11.17 Preventive care, such as regular checking and, if necessary, trimming of hooves, is a very important part of the control of foot problems in ungulates in zoos. Here, an okapi *Okapia johnstoni* at Bristol Zoo is having its hooves cleaned. (Photograph: Mel Gage, Bristol Zoo)

growth is worn down as the animal moves around, but sometimes hoof overgrowth can occur. In the even-toed ungulates (order Artiodactyla), hoof overgrowth may lead to unevenness in weight-bearing on the two claws of each hoof and this can give rise to lameness (as can diseases of the hoof, or dietary deficiencies (see Zuba 2012)). Similar problems of hoof overgrowth can occur in the odd-toed ungulates (order Perissodactyla), such as the equids and rhinoceroses.

In a study of hoof overgrowth in Hartmann's mountain zebra *Equus zebra hartmannae* at Paignton Zoo Environmental Park, UK, Yates and Plowman (2004) found that the zebra were spending less than 8 per cent of their time walking or trotting around the paddock. Of the time spent in locomotion, over 90 per cent was on grass. The hooves of the zebra were not being worn down by sustained contact with an abrasive surface. A change in diet and enclosure layout, to encourage greater locomotion, resulted in the animals both losing weight and also moving around more, causing their hooves to wear down more normally.

Csuti *et al.* (2001) have suggested that foot problems are the most common health care problem in elephants in captivity. Although African elephants *Loxodonta africana* and Asian elephants *Elephas maximus* differ in their number of toenails,[16] both species have a broadly similar foot structure, with a horny pad covering the sole of

---

[16] African elephants have four toenails on their front feet and three on their back feet, whereas Asian elephants (normally) have five nails on the front and four on the back feet (Csuti *et al.* 2001).

Figure 11.18 Captive elephants are particularly prone to foot problems such as cracks in the sole of the foot or in the toenails. This can allow the foot to become infected, so prevention is much better than cure. Photograph (a) is from the archives of the Smithsonian's National Zoo in Washington, DC, and shows a keeper filing the toenails of an elephant under 'free contact' conditions. Photograph (b) shows similar work being carried out under protected contact at Artis Zoo in the Netherlands. Nowadays, most work with zoo elephants is carried out under protected contact, on grounds of keeper safety. (Photographs: (a) Smithsonian's National Zoo; (b) Jeroen Stevens)

the foot (**Fig. 11.18**). Both species of elephant seem to suffer from similar foot problems in captivity, although Schmitt (2003) suggests that these problems are more prevalent in Asian than in African elephants. The most common problems are cracks in the sole of the foot or in the toenails or cuticles, foot overgrowth, injuries, and abscesses. Cracks and injuries to the feet can allow the entry of pathogens, particularly if elephants cannot avoid standing in their own faeces. Usually, these problems are treatable, but they can result in disability or even, in severe cases, death from euthanasia where chronic foot disease does not respond to treatment (Schmitt 2003; Fowler 2006).

Elephants that are housed primarily on hard substrates such as concrete, with little opportunity for exercise, appear to be particularly prone to foot problems. In their comprehensive book, *The Elephant's Foot*, Csuti *et al.* (2001) recommend that zoo elephants should be given plenty of opportunity for exercise and should have enclosures with a variety of substrates (sand, mud, grass, etc.) to minimize the development of foot problems. There is also much useful information in the BIAZA elephant management guidelines (BIAZA 2010b).

Birds

Captive birds which show low levels of activity and spend a high proportion of time perching are considered to be at greater risk of developing bumblefoot or ulcerative pododermatitis (e.g. Samour 2000). This is a serious health problem affecting the feet of many species of captive birds, particularly birds of prey (for example, falcons (Naldo and Samour 2004)); it can also occur in mammals such as rodents. Caused by bacterial infection of the soft tissue of the foot, commonly by *Staphylococcus aureus*, the disease is characterized by the development of swellings and lesions

('bumbles') on the tarsal pads or plantar surface of the foot. If left untreated, bumblefoot can become chronic and invasive, and can lead to disability or even death (Reidarson *et al* 1999).

One of the main preventive measures is managing birds in such as way to increase their overall activity and reduce the amount of time spent perching. In a study of captive Waldrapp or northern bald ibis *Geronticus eremita*, Vargas-Ashby and Pankhurst (2007) found that the introduction of a simple and inexpensive feeding enrichment device led to a significant reduction in the proportion of time the ibis spent inactive on perches, with a corresponding increase in the proportion of time allocated to active behaviours such as walking, flying, and foraging on the ground (unexpectedly, the use of the enrichment device also led to a significant reduction in levels of aggression between individuals within the colony).

11.4.8 Post-mortem examinations

Finding out why an animal has died is part of preventive medicine. The cause of death might be an infectious disease, for example, and this obviously has implications for the health of other animals in the collection. Long-term post-mortem records provide useful data on trends in health, both at individual zoos and among the wider zoo community, and this information can then inform future decisions about health care in living animals.

For example, Hope and Deem (2006) analysed the veterinary records of 172 jaguars *Panthera onca* at thirty AZA member zoos between 1982 and 2002, including post-mortem records. They were able to determine common causes of **morbidity**[17] and mortality, and found, for example, that musculoskeletal diseases were the most common cause of mortality in captive male jaguars. They were able to use the data from their study to make recommendations for the management of jaguars in captivity.

3.15	Adequate facilities must be available either at the zoo or within a reasonable distance for the post-mortem examination of all species held at the zoo
3.16	Dead animals must be handled in a way which minimizes the risk of transmission of infection
3.17	Animals that die at the zoo should be examined post-mortem in accordance with veterinary advice. Where appropriate, samples for diagnosis or health monitoring should be taken for laboratory examination

Table 11.3 Post-mortem examinations (from the Secretary of State's Standards of Modern Zoo Practice* *From Defra (2012a)

In the UK, section 3 of the SSSMZP (Defra 2012a) sets out specific recommendations for post-mortem examinations of zoo animals; these recommendations are shown in **Table 11.3**.

11.4.9 Diet

Ensuring that animals have a proper diet plays a major role in preventive medicine, and where zoos employ a nutritionist, he/she invariably works as part of the veterinary team. (see **Chapter 12**). The key aspects of zoo animal diet in relation to health are providing the right **nutrients**, in the right quantities, with the right sort of food presentation.

11.4.10 Exhibit design

Zoo vets, as well as keepers, may be asked to play a role in the development of new enclosures, contributing advice on safety and welfare issues in relation to enclosure design. Poorly designed enclosures can lead to injury or contribute to the spread of disease (for example, if drainage

---

[17] Morbidity refers to the incidence or prevalence of a particular disease within a population, whereas mortality refers to the proportion of deaths in a population, over a given period of time.

is inadequate). The SSSMZP make a number of health-related recommendations regarding enclosure design, including, for example, a requirement that: '*water-filled and dry moats used for the confinement of animals must provide a means of escape back to the enclosure for animals falling into them*' (Defra 2012a).

Decisions on whether or not animals should be housed in multi-species exhibits may also require veterinary input, particularly if there may be an increased risk of injury or the spread of disease.

11.5 Diseases of concern in zoo animals

A disease may be 'of concern' to zoos either because of the risk of direct losses of animals, or because of the impact on the zoo of required measures in the case of an outbreak (or a combination of these). Each zoo will have different 'diseases of concern', depending on its geographical location and the types of animal in its collection, and these diseases of concern may vary quite widely from collection to collection, and over time. Foot and mouth disease (FMD), for example, was of great concern to zoos in the UK during the outbreak of 2001, but, at the time of writing, blue tongue (a disease that affects **ruminants**) is of particular concern to zoos in the UK and Western Europe.

Health risk assessment provides the basis upon which zoos decide which diseases are important and is a vital part of health care planning for collections. When drawing up a list of diseases of concern, zoo vets must consider both the probable morbidity and mortality from a given disease, and the likelihood of an outbreak; the latter will be based, in large part, on the species held in the collection and previous patterns of disease.

However, diseases can be considered under four broad headings for all zoos. The first three categories, dealt with here, are:

(1) infectious diseases;

(2) degenerative diseases;

(3) genetic diseases.

The fourth category is nutritional diseases; these are mentioned only briefly here and are considered in more detail in the next chapter, on 'Feeding and nutrition' (**Chapter 12**).

11.5.1 Infectious diseases

An infectious disease is a disease caused by pathogenic micro-organisms such as bacteria, viruses, fungi, or parasites, and can (usually) be transmitted from one animal to another. The microorganisms that cause disease, along with proteins such as **prions**, are referred to as 'pathogens' or 'infective agents'. The clinical signs of the disease[18] are caused by either the pathogen itself or its products (for example, the toxins produced by bacteria such as *Escherichia coli* strain O157:H7), or by the body's response to either of these.

Infectious diseases are sometimes also called **communicable diseases**[19], because they can usually be 'communicated', or passed on, between animals or humans. Examples include TB, rabies, and FMD. Infectious diseases can spread via food and water, or by aerosol transmission, **fomite** transmission, or direct physical contact.

Bacterial diseases

Among the main bacterial diseases that can be of concern in zoos are salmonellosis, shigellosis, anthrax, TB, yersiniosis, clostridial diseases, and

---

[18] A 'clinical disease' has recognizable signs, such as fever, a rash, or weight loss, whereas a 'subclinical disease' has no detectable clinical signs. Many diseases can be subclinical for a period of time before the signs become obvious; examples are diabetes and arthritis.

[19] Strictly speaking, infectious and communicable diseases are not quite the same thing. Communicable diseases are infectious diseases which are easily spread from one animal to another (or from one human to another). Not all infectious diseases are communicable; for example, Lyme disease is (nearly always) caused by a bite from an infected tick, rather than passed directly from one human or one animal to another.

campylobacteriosis. The names of these diseases usually reflect the name of the infective agent; salmonellosis, for example, is the name of the disease caused by infection by any of the species of *Salmonella* bacteria, and shigellosis is caused by *Shigella*.

All the diseases mentioned above are also zoonotic; that is, they can be transmitted to humans. **Table 11.4** provides a list of some of the diseases of concern in zoo animals.

Salmonellosis

Salmonella presents two challenges in terms of animal health care. Firstly, *Salmonella* bacteria are unusual, in that they can live and multiply outside a host organism (for example, on, or in, contaminated food). Secondly, animals can be asymptomatic carriers.

There are a very large number of species of *Salmonella* bacteria that cause disease (Ketz-Riley 2003), but not all *Salmonella* spp. can infect all hosts. For example, typhoid fever in humans, caused by *S.typhosa*, does not occur naturally as a disease in non-human primates. However, *S.enteriditis* and *S.enterocolitis* are commonly isolated pathogens in a range of vertebrate zoo animals, and cause diarrhoea, which may be severe. Septicaemia can be a (potentially fatal) complication of infection by *Salmonella* spp.

Several *Salmonella* spp. are pathogens in reptiles, and salmonellosis is an increasingly reported problem in captive exotic reptiles held outside zoos, as pets. For example, all **chelonid** species are susceptible to *Salmonella* infection; many reptiles will be asymptomatic carriers of *Salmonella* spp. (Raphael 2003) (**Fig. 11.19**).

Shigellosis

Like *Salmonella*, *Shigella* has a worldwide distribution and the main transmission route is faecal–oral. Along with *Campylobacter*, it is a frequently isolated pathogen in zoo primates; the disease usually presents in primates as an acute gastrointestinal infection.

The most commonly found *Shigella* spp. in non-human primates is *S.flexneri* (Ketz-Riley 2003).

Tuberculosis

Tuberculosis is the collective name given to infection with bacteria in the genus *Mycobacterium* (Mikota 2007). All mammalian species are susceptible to TB, and some taxa, such as the non-human primates, are highly susceptible. In zoos, however, most animals are not regularly subjected to blood sampling, and so it is difficult to know which animals may be carriers of this disease. TB is also a zoonosis.

Figure 11.19 Reptiles such as these snakes (a dark and an albino form of the Burmese python *Python molurus bivittatus*) can be asymptomatic carriers of *Salmonella*, which is a zoonosis and can cause serious illness and even fatalities in humans. Sensible hygiene precautions, such as thorough hand-washing before and after handling reptiles, reduce the risk of disease transmission. (Photograph: Jeroen Stevens)

Disease	Causative pathogen	Distribution	Transmission route	Symptoms	Susceptible taxa
Anthrax*	*Bacillus anthracis*, bacterium	Worldwide (rare in the UK and Europe; more common in warmer climates)	Infected carcasses; ingestion of spores (for further details, see de Vos 2003)	Ruminants may die suddenly without showing prior symptoms; in other taxa, symptoms include swelling of the face, throat, and neck	Most mammals and occasionally birds, e.g. ostriches (see Bengis 2012)
Aspergillosis	*Aspergillus* spp., fungi	Worldwide	Inhalation	Usually diagnosed post-mortem (often an opportunistic infection in stressed/immunosuppressed animals)	Frequently occurs in birds (see Cray 2012)
Avian influenza (bird flu) (see **section 11.5.4**)	Influenza A virus (the A does not stand for 'avian'). The highly pathogenic strain of current concern is H5N1	Worldwide	Direct contact with faeces; aerosol	Highly variable and can be asymptomatic; often clinical signs of respiratory disease	Birds, but can also infect mammals (including humans); waterfowl may be reservoirs for the virus (see Cook and Karesh 2012; Gilbert and Phillipa 2012)
Bovine spongiform encephalopathy (BSE) and other transmissible spongiform encephalopathies (TSEs)	The infectious agent is not a pathogen, but a protein known as a prion	Probably worldwide	Contact with and/or consumption of infected tissue	Unsteady gait, involuntary jerky movements	Bovids (BSE); felids (other TSEs) Scrapie in sheep and goats, and chronic wasting disease (CWD) in cervids are also prion diseases
Bumblefoot (ulcerative pododermatitis)	Bacterial infection, commonly *Staphylococcus aureus*	Worldwide	Direct contact with faeces, often linked to a high proportion of time spent perching (birds) or standing on wire floors (rodents and lagomorphs)	Development of swellings and lesions ('bumbles') on feet, particularly on the tarsal pads in birds and the plantar surface in rodents/lagomorphs	Birds, particularly birds of prey, and also mammals such as rodents and lagomorphs

Campylobacteriosis	*Campylobacter* spp., bacteria	Worldwide (the incidence of campylobacteriosis worldwide is increasing rapidly)	Waterborne (also via milk)	Diarrhoea, loss of appetite, occasional vomiting; can be asymptomatic	A wide range of mammals, particularly bovids, and birds
Candidiasis	*Candida* spp., fungi	Worldwide	*Candida* spp. are normal residents of the intestine; disease occurs when the usual balance of the gut flora is upset	Usually affects the GI tract; infected birds may show weight loss or regurgitation	Birds, mammals (often an opportunistic infection and may follow a period of antibiotic treatment)
Chlamydiosis/ chlamydophilosis	*Chlamydia* and *Chlamydophila* spp. (see Flammer (2003) for information about changes to the taxonomy of the Chlamydiaceae)	Worldwide	Close contact with an infected animal (may be an asymptomatic carrier); aerosol transmission; contaminated fomites; insect vectors	Weight loss, listlessness, ruffled feathers in birds; also diarrhoea and respiratory symptoms (the clinical symptoms of chlamydiosis vary widely)	In zoos, chlamydiosis is most common in birds, but it can occur in a wide range of vertebrate and invertebrate taxa (Flammer 2003)
Clostridial diseases (see also entry for tetanus)	*Clostridium* spp., bacteria, particularly *C.perfringens*	Worldwide	Faeces	Usually enteritis (diarrhoea, dysentery); some forms of the disease can cause rapid death	Most mammals and birds (isolated from some reptiles, but does not appear to cause disease)
Colibacillosis	*Escherichia coli,* bacterium; many hundreds of different serotypes exist, of which only a few are pathogenic	Worldwide (*E.coli* bacteria are a normal part of the intestinal flora of mammals and birds)	Faeces, particularly faecal contamination of foodstuffs	Enteric disease (diarrhoea, dysentery)	Mammals, particularly ruminants, and birds

Disease	Causative pathogen	Distribution	Transmission route	Symptoms	Susceptible taxa
Cryptosporidiosis	*Cryptosporidium* spp. (e.g. *C.parvum* in ruminants); microscopic protozoan parasite	Worldwide	Direct contact, particularly with faeces; ingestion of contaminated water or food	Often asymptomatic; symptoms include diarrhoea, which may be mild	Ruminants, primates, canids, felids, rodents
Equine encephalomyelitis* (also referred to as equine encephalitis)	Arboviruses (several strains)	North, Central, and South America	Mosquitoes and other biting insects (birds and small mammals are the hosts)	Symptoms include impaired CNS function such as gait problems and head pressing; mortality can be high.	Equids
Foot and mouth disease (FMD)	Virus	Africa, Asia, South America; outbreaks occur outside these areas (e.g. in the UK in 2001)	Direct contact	Fever, lameness, and characteristic blistering (vesicle formation) in the mouths of infected animals; not usually fatal	Ungulates; some other mammalian taxa, including elephants
Glanders and farcy* (glanders and farcy are two forms of the same bacterial disease)	*Burkholderia mallei*, bacterium	Once prevalent worldwide; now eradicated from many countries including the USA and UK	Ingestion of, or contact with, contaminated food or water	Disease of the skin (farcy) and respiratory tract (glanders); symptoms include nasal discharge, coughing and fever, or subcutaneous nodules	Equids (not in the UK, where glanders has been eradicated)
Hepatitis (viral) (the word hepatitis means inflammation of the liver; not all cases are due to a viral infection)	Various forms of hepatitis virus, such as hepatitis A and B (hepatitis B only infects humans and the great apes)	Worldwide (not all types are found in all countries)	Captive primates can catch hepatitis A from infected humans; other forms of hepatitis can be transmitted via contact with faeces or contaminated food	Lethargy, jaundice, vomiting, but can be asymptomatic; may be fatal (as a result of liver failure)	Primates (some other taxa can be infected by hepatitis viruses or by the similar hepadna viruses)

Herpesviruses (see **section 11.5.1** on herpes B virus in primates)	Various herpesviruses	Worldwide	Direct contact including sexual transmission; aerosol	Very variable—from asymptomatic carriers to severe disease and death	Mammals and birds
Leptospirosis	*Leptospira* spp., bacteria	Worldwide	Direct or indirect contact with infected urine, placental fluids, or milk (Bolin 2003)	Clinical signs very variable; can include fever, vomiting, diarrhoea, and death	Most mammals
Listeriosis	*Listeria monocytogenes*, bacterium	Worldwide	Ingestion of contaminated food	Abortion; meningitis in young animals	Many mammals; all primates appear to be susceptible to infection
Lumpy jaw or *Actinomycosis*	*Actinomyces* spp., bacteria	Worldwide	Direct contact; infection often arises after a penetrating injury	Swelling of the jaws (usually; can occur in other areas of the body) and formation of abcesses	A wide range of mammalian taxa, including macropods
Lyme disease or Lyme borreliosis (this is a vector-borne disease)	Bacteria from the genus *Borrelia*	Widespread, particularly in Europe and North America	Transmitted by ticks carried by a range of hosts including mammals, birds, and reptiles	Lameness, sometimes accompanied by fever	A range of mammals, particularly deer; mouse species are often a reservoir host
Malignant catarrhal fever (MCF)	Virus infection by one of a number of ruminant gammaherpesviruses	Worldwide	Direct or aerosol transmission	Fatal in some species such as bison and some deer species	This disease poses a particular risk in mixed species exhibits of ungulates (Kaandorp 2012)

Disease	Causative pathogen	Distribution	Transmission route	Symptoms	Susceptible taxa
Measles	Rubeola virus (morbillivirus)	Worldwide	Measles can also be transmitted from humans to primates, i.e. it is anthropozoonotic	Skin rash, fever; can be fatal	Great apes (see Hastings *et al.* (1991) for an account of the diagnosis and treatment of measles in wild mountain gorillas)
Mycobacteriosis (see separate entry for *M.tuberculosis,* under Tuberculosis)	*Mycobacterium* spp., bacteria, e.g. *M.avium* in birds	Worldwide	Usually ingestion, but also inhalation	Usually a chronic disease	Birds, mammals, amphibians (see Chai (2012) for an account of mycobacteriosis in amphibians)
Plague	*Yersinia pestis,* bacterium	Parts of Asia, Africa, and the Americas	Transmitted by rodents and their associated fleas	Plague has three main clinical forms: bubonic, septicaemic, and pneumonic (for details of the signs of each of these forms, see Williams (2003))	A wide range of mammalian species
Pox diseases	Poxviruses such as monkey-pox, cowpox, camel-pox, etc.	Worldwide	Direct contact; bites and scratches	Skin disease (lesions and tumours); can be fatal	Mammals, birds, and reptiles (see Greenwood (2003) and, for cowpox, Kurth and Nitsche (2012))
Rabies*	*Lyssavirus* spp. (the diseases produced by any *Lyssavirus* infection are indistinguishable from 'classic' rabies (Calle 2003))	Worldwide, except Australia and Antarctica; 'classic' rabies is absent from the UK, but British Chiroptera spp. can carry bat lyssaviruses	Bites from an infected animal; occasionally scratches	Initial signs include lethargy, loss of appetite and fever, followed shortly by ataxia and nervous system dysfunction; rabies is nearly always fatal.	A number of vertebrate animals, including felids and canids; also Chiroptera (bats)

Ringworm	*Microsporum* spp./ *Trichophyton* spp., fungal infection	Worldwide	Direct contact with infected animals or fomites	Hair loss; skin crusting; sometimes pruritus	Wide range of vertebrates, particularly canids and other Carnivora; also Chiroptera (bats)
Salmonellosis	*Salmonella* spp., bacteria, e.g. *S.enteritis* (more than 2,000 serotypes have been identified)	Worldwide	Usually ingestion, sometimes inhalation (e.g. of contaminated feather dust); vertical transmission (bird to egg) can occur	Symptoms range from mild enteritis to severe diarrhoea, septicaemia, and sometimes death	Many mammals, birds, and reptiles
Sarcocystosis	*Sarcosystis* spp., protozoan parasite.	North America	Faeces (opossums are the only known definitive host (Lamberski 2003))	Variable; infected birds may show pneumonitis	*S.falcatula*—birds, particularly psittacines *S.neurona*—mammals, including seals, otters, skunks, and felids
Shigellosis	*Shigella* spp., gram-negative rod bacteria	Worldwide	As with salmonellosis, the transmission route is faecal–oral	Diarrhoea to severe bloody dysentery (some animals may be asymptomatic carriers)	All primates are susceptible, particularly during periods of stress, e.g. introduction into a new social group
Tetanus	*Clostridium tetani*	Worldwide	Spores may enter wounds in the body	Stiffness and spasms; can be fatal	Ruminants, such as cervids

Disease	Causative pathogen	Distribution	Transmission route	Symptoms	Susceptible taxa
Tuberculosis* (infection with *Mycobacterium* spp. other than *M.tuberculosis* is referred to as 'mycobacteriosis'; see separate entry)	*Mycobacterium tuberculosis*, bacterium	Worldwide	Close contact with infected humans (particularly aerosol transmission via coughing or expectoration)	Coughing, nasal discharge, loss of appetite and weight loss, low fever	Primates, elephants, and some other mammals Other *Mycobacterium* spp. can infect a wide range of vertebrates
West Nile virus (WNV) (see **section 11.5.4**)	WNV is an arbovirus in the family Flaviviridae (some texts refer to WNV as a flavivirus) (Travis 2007)	Europe, Africa, Asia, Middle East; North America from 1999	Blood-feeding biting insects (e.g. mosquitoes, sandflies) (see Travis 2007)	Usually diagnosed post-mortem	Birds; some mammals, including humans and equids, are susceptible if bitten by an infected insect
Yersiniosis	*Yersinia* spp., particularly *Y.pseudotuberculosis* and also *Y.enterocolitica*, bacteria (*Y.pestis* is the pathogen that causes plague)	*Y.pseudotuber-culosis* is found worldwide	Contaminated foodstuffs (faecal contamination); insects, such as cockroaches, may also be important vectors for transmission	Listlessness, weakness; death can occur within 48 hours; sudden death with no prior clinical symptoms can also occur	Mammals, many bird species, some reptile and fish species; in zoos, New World primates and some bird species appear to be particularly vulnerable (Allchurch 2003)

Table 11.4 Diseases of concern: common and/or important infectious diseases of zoo animals (for a list of major zoonoses of zoo animals, see **Table 11.5**)

*Indicates a notifiable disease in the UK (a notifiable disease is a disease named in section 88 of the Animal Health Act 1981; not all notifiable diseases are zoonotic). Any outbreak of a notifiable disease must, by law, be reported to the police; in practice, Defra should also be notified.

Note: This list is not exhaustive and excludes most of the very large number of diseases caused by endoparasites, such as hookworms, whipworms, lungworms, flukes, etc. See Fowler and Miller (1999; 2003; 2008; 2012) for further information about disease in zoo and wild animals. Jackson (2010) provides useful information about diseases, including parasitic diseases, for the Australian mammalian fauna.

Elephants are also susceptible to both strains of TB, but particularly the human strain, *M.tuberculosis*. A number of cases of TB in elephants in captivity in the USA in the 1990s led to the setting up of a National Tuberculosis Working Group for Zoo and Wildlife Species and the production of *Guidelines for the Control of TB in Elephants* in 1997 (Mikota *et al.* 2000; Mikota 2007). These guidelines, which can be downloaded from the website of the US Animal and Plant Health Inspection Service (APHIS), were revised in 2000 and again in 2003, as knowledge of the diagnosis and treatment of TB in elephants improved.

For further reading on TB in elephants, the proceedings of the Elephant Tuberculosis Research Workshop held in Orlando, Florida, in 2005 provide an excellent starting point. The proceedings of this workshop can be accessed via the website of the organization Elephant Care International, which also contains links to the current TB guidelines.

Viral diseases

Viral diseases that can arise in zoo animals include rabies, herpes, and various diseases caused by poxviruses (see **Table 11.4**). (West Nile virus is dealt with in more detail in **section 11.5.4**).

Rabies

Rabies is the general term used for a disease of mammals caused by infection with viruses from the *Lyssavirus* genus (Calle 2003). Once clinical signs of rabies appear, it is nearly always fatal. Worldwide, rabies is a serious zoonosis, causing tens of thousands of human deaths each year. Because of the risk to human life, together with the long incubation period of the disease (weeks to months), many countries have stringent rabies quarantine regulations. In the UK, for example, the quarantine period for rabies is four months (see **section 11.4.2** for more information about quarantine regulations).

Figure 11.20 There are many different poxviruses that can cause disease in zoo animals (for example, cowpox and monkeypox). This grey seal *Halichoerus grypus* is infected with a poxvirus, which produces unsightly lumps but is usually only a mild infection in these animals. (Photograph: Sheila Pankhurst)

Within North American zoos, free-ranging wild animals have been found to be infected with rabies; *Lyssavirus* infection has been recorded in captive fruit bats in a **walk-through exhibit** at Rotterdam Zoo in the Netherlands (Mensink and Schafternaar 1998).

In Europe, four human deaths from bat *Lyssavirus* infection have occurred since 1977 (Fooks *et al.* 2003).

Poxvirus infections

Poxvirus infections give rise to generalized skin disease and skin tumours (Greenwood 2003) (**Fig. 11.20**). Poxvirus infections can occur in mammals (for example, cowpox and sealpox) and in birds (for example, avian pox), and can be fatal in some species. The mortality rate for cowpox, in particular, among exotic animals is high (Kurth and Nitsche 2012). A poxvirus-like infection has also been reported for captive crocodilian species, but the so-called carp pox in fish is caused by a herpesvirus[20].

Herpesviruses

Herpes B or, more correctly, cercopithecine herpesvirus 1 (sometimes called simian herpesvirus),

---

[20] Veterinary and medical texts usually refer to herpesviruses (all one word) whereas the media and lay text often separate the term into two words. Both are correct.

is a zoonotic virus found in monkeys belonging to the genus *Macaca.* Clinical signs in monkeys such as the rhesus macaque *Macaca mulatta* are often quite mild, but the disease is a serious zoonosis that can cause fatal encephalitis in humans (Fowler and Miller 2003; Richman 2007). Diagnosis of the disease is problematic, because infected monkeys may be asymptomatic (Richman 2007) and the virus is difficult to distinguish from the related herpes simplex virus (HSV).

Richman and Hayward (2012) have reported a newly recognized disease in elephants—elephant endotheliotropic herpesvirus (EEHV)—which can be fatal. Herpesviruses are also significant pathogens of tortoises, with high mortality rates for infected animals (Johnson *et al.* 2005).

Fungal diseases

Fungal pathogens that can cause health problems in zoos include *Aspergillus*, *Candida*, *Cryptococcus*, and *Pneumocystis* (see **Table 11.4**). As with bacterial diseases, the name of the disease usually reflects the name of the infective agent, with *Candida* giving rise to candidiasis, *Aspergillus* to aspergillosis, and so on. Fungal diseases, particularly candidiasis, are often associated with general ill health, immunosuppression, or a long period of treatment with antibiotics (Duncan 2003). Aspergillosis can be a serious problem in captive birds. For example, Flach *et al.* (1990) recorded aspergillosis as the most common cause of death in gentoo penguins *Pygoscelis papua* at Edinburgh Zoo between 1964 and 1988.

Ringworm

Ringworm (dermatophytosis) is fungal disease of the skin and is also a zoonosis. The infective agents are *Microsporum* and *Trichophyton* spp. in non-human animals, and *Epidermophyton* in humans (Duncan 2003). Among zoo animals, the felids and canids are particularly susceptible to ringworm infection.

Parasitic infections

The control of parasites in zoo animals has already been considered briefly in this chapter (**section 11.4.6**). Health problems caused by ectoparasites in zoo animals include warble fly and scabies (or sarcoptic mange); diseases caused by endoparasites include toxoplasmosis and avian malaria.

Warbles

Warbles, or hypodermosis, is rare in the UK following an extensive eradication campaign, but is still common in other parts of the world. Warble flies lay their eggs on the skin of the host animal. The eggs hatch and the larvae burrow into the animal, remaining under the skin of the host for several months (visible in later stages as lumps, or warbles, on the animal, usually along the back). There are a number of different species of warble fly worldwide; the two species found in the UK both belong to the genus *Hypoderma*.

Bovid species infected with warbles can be treated with the topical application of drugs such as ivermectin.

Scabies (sarcoptic mange)

Scabies is caused by a mite, *Sarcoptes scabiei*, which burrows into the skin of its host to lay its eggs, causing mange. Scabies is most common in ungulates, but can occur in a wide range of mammalian species, including primates. This parasitic infection can also be treated with ivermectin, either topically or orally.

Toxoplasmosis

Most vertebrates, including humans, are susceptible to infection by the **coccidian parasite** *Toxoplasma gondii* (Wolfe 2003). However, infected animals may be asymptomatic or show only mild signs, and susceptibility varies considerably with both the strain of the parasite and the **taxonomic** group of the infected species. Australian marsupials and New World monkeys, for example, are highly susceptible to severe toxoplasmosis, whereas Old World monkeys, cattle, and horses are relatively resistant to the disease.

Domestic cats, whether feral or pets, are the definitive host for toxoplasmosis; other infected vertebrates are intermediate hosts. Toxoplasmosis

can cause abortion and stillbirth during gesta-
tion, and the disease is a significant cause of fetal
mortality in sheep and goats; infection in humans
during the first trimester can also be lethal to the
developing fetus (Wolfe 2003).

Avian malaria

Avian malaria, transmitted by mosquitoes of
the *Culex* spp., is a major cause of mortality in
outdoor-exhibited penguins in zoos and wildlife
parks (Graczyk *et al.* 1995) (**Fig. 11.21**). The in-
fective organisms for this disease are the parasite
species *Plasmodium relictum* and, to a lesser ex-
tent, *P.elongatum*. In their natural habitat, most
penguin species inhabit regions where there are
few, if any, mosquitoes, so avian malaria is not an
important disease of wild penguins.

Avian malaria is not only a disease of penguins,
but also occurs in other bird taxa, particularly in
non-indigenous falcons (Redig and Ackermann
2000). It is possible to treat birds prophylactically
with anti-malarial drugs, such as primaquine or
mefloquine, administered during the main in-
sect season. A new DNA-based 'third-generation'
vaccine against avian malaria has had promising
results in initial trials although, at present, an an-
nual booster injection is needed (Cranfield *et al.*
2000; Grim *et al.* 2004).

Figure 11.21 Outdoor-housed penguins, such as
these Humboldt's penguins *Spheniscus humboldti*,
are susceptible to infection with avian malaria, which is
transmitted by mosquitoes. This can be a serious, and
sometimes fatal, illness in zoo birds, occurring not only in
penguins, but in a range of avian species. (Photograph:
Sheila Pankhurst)

11.5.2 Degenerative, genetic, and nutritional diseases

Degenerative diseases

Degenerative diseases, such as arthritis and
chronic renal disease, are relatively common in
felids, canids (e.g. Rothschild *et al.* 2001), bears,
primates, and ruminants, all of which are well
represented in most zoo collections. These dis-
eases are often age-related and can pose a par-
ticular problem in zoological collections, because
animals such as bears and large cats may live
longer in zoos than they would in the wild (e.g.
Shoemaker 2005).

Other health problems associated with age-
ing animals include dental problems—teeth can
become worn down, so that the animal can no
longer feed effectively—and diseases such as dia-
betes and arthritis. These are largely diseases of
captivity; wild animals with diabetes or arthritis,
or with badly worn-down teeth, would not survive
for long.

Genetic diseases and health problems

By definition, zoo populations of some endan-
gered species are likely to be small and the **gene
pool** may be restricted. Although the use of stud-
books (see **Chapter 9**) limits inbreeding, genetic
abnormalities do occur in zoo animals (Leipold
1980). However, these are rare. Previously noted
examples include black-and-white ruffed lemurs
Varecia variegata variegata in zoos, where a
number of congenital abnormalities have been
recorded, including **scoliosis** and skull abnormal-
ities (Benirschke *et al.* 1981). In grey or timber
wolves *Canis lupus*, a hereditary form of blind-
ness appears to be linked to inbreeding (Laikre
and Ryman 1991).

Nutritional diseases

Common nutrition-related health problems in
zoo animals include metabolic bone disease, iron
storage disease (haemochromatosis), and ema-
ciation or, more commonly, obesity. These nutri-
tional problems are considered in more detail in
Chapter 12.

11.5.3 Zoonoses, anthropozoonotic diseases, and notifiable diseases

Zoo animals can catch some diseases from humans—and vice versa. Diseases that are transmitted from humans to animals are known as **anthropozoonotic diseases** (Ott-Joslin 1993), whereas diseases transmitted from animals to humans are zoonoses (or zoonotic diseases). The latter form a much longer list than the former, but this is, in part, because we do not yet know as much about the transmission of human diseases to exotic animals. Schwabe (1984) suggests that it is likely, for the apes at least, that these animals are susceptible to many, if not most, human diseases (**Fig. 11.22**).

A disease that shows very similar pathology in both humans and animals is referred to as an **isozoonosis**. **Table 11.5** lists some of the major zoonoses that can be transmitted to humans from exotic animals.

The transmission of zoonoses is via direct contact with an infected animal, or via ingestion or inhalation of pathogens, or by being bitten by an insect such as a mosquito. Most reported cases of zoonoses arising from zoo animals are among the zoo professionals who come into close physical contact with the animals on a daily basis, rather than among zoo visitors. Good hygiene is the most important control measure for zoonoses (for example, washing hands after handling animals).

Notifiable diseases

A notifiable disease is a disease that, by law (in the UK), must be reported to the police; in practice, Defra should also be notified. Notifiable diseases within the UK are named in section 88 of the Animal Health Act 1981; some, but not all, of these are zoonotic. In the UK, the government agency responsible for managing notifiable diseases is called the **Animal Health Veterinary Laboratories Agency (AHVLA)**, and is an executive agency of Defra. The AHVLA was formed in 2011, following the merger of Animal Health and the Veterinary Laboratories Agency (VLA), and works '*to prevent and control animal disease across Great Britain*' (see **http://www.defra.gov.uk/ahvla/**).

Examples of notifiable diseases within the UK include anthrax, bluetongue, and avian influenza ('bird flu'). There is a useful table on the Defra website summarizing these diseases (see **http://www.defra.gov.uk/animal-diseases/**).

In North America, similar information is provided by the Centers for Disease Control and Prevention (CDC) (see **http://www.cdc.gov**), and in Australia the Communicable Diseases Network Australia (CDNA) provides oversight.

Figure 11.22 These lowland gorillas *Gorilla gorilla gorilla* at Apenheul Primate Park in the Netherlands are in good health, but all the great apes are susceptible to infection with human diseases. Diseases that can be transmitted from humans to animals are known as anthropozoonotic diseases; examples include measles and tuberculosis. (Photograph: Sheila Pankhurst)

11.5.4 Three 'headline' diseases

Three very different diseases of domestic or wild animals have attracted considerable press coverage over recent years. These examples of 'headline'

Disease/causative pathogen	Transmission route (to humans)	Animal host(s)	Notes on disease in humans
Anthrax*/*Bacillus anthracis*, bacterium	Ingestion of spores; direct contact with infected animal (or animal hide) (see de Vos 2003)	Wide range of species (mainly herbivorous mammals, some bird species); anthrax infection is very rare in the UK	Anthrax is a rare disease in humans The most common form of the disease is the cutaneous form, contracted via contact with infected animals or their hides; this form of the disease is readily treatable with antibiotics
Avian influenza (AI)* (bird flu)/ influenza A viruses (see **section 11.5.4**	At the time of writing, almost all human cases of AI have been the result of direct contact with infected birds or faecal matter from infected birds	Birds, particularly poultry, and domestic cats; cases of AI have also been reported in non-domestic felids (tigers and leopards) in zoos in Asia	The situation regarding AI is changing rapidly; in the UK, the Defra website provides regular updates on this disease.
Bovine spongiform encephalopathy (BSE)*/prion (protein)	Consumption of infected meat	Bovids	There is no evidence of any link between cases of variant Creuztfeldt–Jakob disease (vCJD) (the human form) and zoo animals
Brucellosis*/*Brucella* spp., bacteria	Consumption of dairy products, such as milk, from infected animals; direct contact, inhalation	Bovids, particularly cattle; more rarely, cervids and other mammals	May be asymptomatic in humans; fever with fluctuations in temperature is characteristic, giving the disease its alternative name of 'undulant' fever
Campylobacteriosis/ *Campylobacter* spp., bacteria	Waterborne (also via milk)	A wide range of mammals, particularly bovids, and birds	In humans, infection can cause a severe form of food poisoning; the incidence of campylobacteriosis in humans has increased greatly in recent years
Cryptosporidiosis/ *Cryptosporidium parvum*, microscopic parasite	Direct contact, particularly with faeces; ingestion of contaminated water or food	Ruminants	Infection in humans generally gives rise to diarrhoea; the disease can be very serious, or even fatal, for immunocompromised patients
Equine encephalomyelitis*/ several strains, virus	Mosquitoes and biting flies	Birds and small mammals are the hosts; mosquitoes or biting flies transmit the disease to humans/equids	This is a mosquito-transmitted disease—it is not directly contagious between equids and humans

Disease/causative pathogen	Transmission route (to humans)	Animal host(s)	Notes on disease in humans
Escherichia coli/ various strains, bacteria	Faeces	Found in the guts of animals, particularly bovids	Strains such as O157 produce a toxin (verocytotoxin) which can cause serious illness and even death in humans
Glanders and farcy*/*Burkholderia mallei*, bacterium	Open wounds	Equids	This disease has been eradicated from the UK, but remains a serious zoonosis in other parts of the world, such as the Middle East and China
Hantavirus pulmonary syndrome (HPS)	Airborne—inhalation of aerosolized virus from urine, saliva, or faeces of infected rodents	Rodents	Very rare in the UK and rare in North America, but cases are often fatal
Hepatitis (viral)	Direct contact with body fluids	Primates	Causes fever, anorexia, and jaundice
Herpes B/virus (simian herpesvirus) (see **section 11.5.1**)	Bites from infected animals	Primates of the genus *Macaca* (macaques)	Herpes B can cause fatal encephalitis in humans
Hydatid disease/*Echinococcus* spp., helminth (tapeworm) parasite	Ingestion of parasite eggs	Canids, via sheep (e.g. where dogs or foxes have been fed raw offal)	Various symptoms, including jaundice; occasionally fatal if cyst ruptures
Leptospirosis/*Leptospira* spp., bacteria	Skin/wound or mucous membrane contact with infected urine	Most mammals, but particularly associated with rodents, such as rats and mice	Killed vaccines against leptospirosis are available in the USA and some other countries for animal use (e.g. for animals in petting zoos)
Listeriosis/*Listeria monocytogenes,* bacterium	Ingestion	Many animals, particularly ruminants	Causes fever, nausea, and diarrhoea; can be fatal

Monkeypox virus belonging to the orthopoxvirus group	Direct contact with an infected animal	Primates, such as gibbons, chimpanzees, and orang-utans	Causes symptoms similar to smallpox in humans; treatment of the disease in humans with cidofovir has been effective
Plague/*Yersinia pestis*, bacterium	Fleas; inhalation; contact with infected animals	Mammals such as rodents (particularly rats); also cats and dogs	Plague is not a major problem in Europe, but still occurs in Central and South America and in Southeast Asia and southern Africa
Psittacosis/*Chlamydophila psittaci* (formerly *Chlamydia psittaci*), bacterium**	Aerosol; inhalation of dust from faeces or feathers; direct contact	Parrots (psittacines), pigeons, poultry, and waterfowl	*C.psittaci*, found in captive parrots, pigeons, and waterfowl, is responsible for most reported cases of zoonotic infection by *Chlamydophila/ Chlamydia* bacteria, although other species can also be zoonotic
Q fever/*Coxiella burnetii*	Aerosol; also via milk	Bovids	
Rabies*/*Lyssavirus* spp., viruses	Saliva of an infected animal, via a bite (or, more rarely, a scratch)	A number of vertebrate animals, including felids and canids	Fatal in humans (rabies is responsible for tens of thousands of human deaths worldwide each year, usually after bites from infected dogs)
Rift Valley fever/virus*		Bovids	Rarely fatal
Ringworm/*Microsporum* spp., *Trichophyton* spp., and *Epidermophyton* spp., fungal infection	Direct contact with infected animals or fomites	Wide range of vertebrates, particularly canids and other Carnivora; also Chiroptera (bats)	Common zoonosis, caused by a fungal infection; rarely serious and usually easy to treat
Salmonellosis/*Salmonella* spp., bacteria	Contaminated food or surfaces; direct contact with infected animals/faeces	Many mammals, birds, and reptiles	Very common source of food poisoning
Shigellosis/*Shigella* spp., bacteria	Faecal/oral transmission (as for salmonellosis)		As with salmonellosis, food poisoning (acute GI infection)

Disease/causative pathogen	Transmission route (to humans)	Animal host(s)	Notes on disease in humans
Toxocariasis/*Toxocara* spp., parasite (roundworm)	Direct contact with an infected animal	Canids and felids	
Toxoplasmosis/*Toxoplasma gondii*, protozoan parasite	Ingestion (of oocysts)	Mammals, especially cats; also birds	Serious if contracted during pregnancy; can cause abortion/stillbirth
Tuberculosis*/*Mycobacterium tuberculosis*, bacterium	Inhalation (particularly of aerosolized fluids from coughing or expectoration)	Primates, less commonly other mammals	TB infection in humans is of increasing concern because of the spread of strains resistant to drugs
West Nile virus	Mosquitoes and other biting insects	Birds and equids	Spread by infected mosquitoes
Yersiniosis/*Yersinia* spp., bacteria, particularly *Y.enterocolitica* and *Y.pseudotuberculosis*	Contaminated food including milk	*Y.pseudotuberculosis* is widespread in mammals, birds, reptiles, and fish (many species appear to be asymptomatic carriers)	

Table 11.5 Major zoonoses of zoo animals

*Indicates a notifiable zoonotic disease in the UK (a notifiable disease is a disease named in section 88 of the Animal Health Act 1981; not all notifiable diseases are zoonotic). Any outbreak of a notifiable disease must, by law, be reported to the police; in practice, Defra should also be notified.

**There are several *Chlamydia* and *Chlamydophila* spp. of bacteria; these cause disease in animals referred to as chlamydiosis or chlamydophilosis (see Flammer 2003).

Note: This table lists some of the major zoonotic diseases (disease transmissible to humans) in zoo animals. The animal health pages of the Defra website provide much useful information, particularly about notifiable diseases (**http://www.defra.gov.uk/animal-diseases**), as does the website of the World Organization for Animal Health (OIE) (**http://www.oie.int**). Janssen (2012) provides general guidelines for the management of zoonotic diseases in zoos, and James (2012) discuss the risks and management of zoonoses in children's zoos or 'petting zoos'.

diseases, all of which have potentially serious implications for zoos, are:

- West Nile virus (WNV);
- avian influenza (AI) or bird flu;
- chytrid fungus in amphibians.

In the UK, outbreaks of bluetongue and Schmallenberg virus have also hit the headlines in recent years; the latter is not considered a major threat to zoo animals, but bluetongue (which affects ruminants) poses a significant risk of mortality and debilitating disease. However, recent work suggests that vaccination against bluetongue is both safe and effective in a range of non-domestic ruminants (Sanderson 2012), and Defra issued a general licence for this purpose in the UK in 2012.

West Nile virus

WNV hit the headlines in 1999, when it was isolated for the first time in the USA. The virus, which is zoonotic, was identified by pathologists at the Bronx Zoo in New York, after the death of a number of birds at the zoo (Steele *et al.* 2000). WNV is transmitted largely by arthropods, such as mosquitoes and other biting insects, but can also be transmitted by direct contact with infected animals or tissue from infected animals (Travis 2007). Although the disease has been known in Asia, Africa, and southern Europe for many decades, it had not been isolated in animals in the Americas prior to 1999.

Humans[21] and a wide range of vertebrate species—but particularly birds and horses—are susceptible to WNV, which causes potentially fatal encephalitis. Among zoo mammals, cases of WNV have been reported in animals ranging from an Arctic wolf *Canis lupus* to reindeer *Rangifer tarandus* (Travis 2007).

A vaccine against WNV is currently available for horses, and new vaccines are in development.

[21] Since 1999, more than 700 human deaths from West Nile virus have been reported in the USA (Travis 2007).

Protective measures against the disease include spraying with insecticides to kill adult and larval mosquitoes (Travis 2007).

Avian influenza

AI (or bird flu) is an infection in birds caused by influenza viruses that are very similar to human influenza viruses. The disease is carried by wild birds—particularly ducks and other wildfowl which may not develop the disease themselves, but can transmit the virus via their faeces to domestic poultry and other captive birds (**Fig. 11.23**). AI is of concern to zoos not only because of the risk to birds in their collections, but also because the virus can infect a range of mammalian species, from mice, pigs, monkeys, and ferrets, to felids,

Figure 11.23 Avian influenza is a disease that can be transmitted to captive birds by wild birds. Preventing wild birds from gaining access to zoo enclosures is an important preventive measure to stop its transmission, but this is very difficult to do in the case of outdoor-housed zoo birds such as these black swans *Cygnus atratus*. (Photograph: Warsaw Zoo)

such as tigers and leopards. For example, at a private zoo in Thailand in 2004, where tigers were fed infected chicken carcasses, forty-five animals died from the disease (Amosin *et al.* 2006). Gilbert and Philippa (2012) provide a summary of documented outbreaks of the highly pathogenic strain of AI in zoos around the world.

Different strains of AI are categorized either as 'low pathogenic' (LPAI) or 'highly pathogenic' (HPAI). The most recent outbreak (2003 onwards) of bird flu is of the H5N1 strain, which is both highly contagious and highly pathogenic; domestic birds, such as chickens and ducks, can die from the virus within 24 hours of clinical signs first appearing.

Information about AI rapidly becomes out of date, so the reader is referred to websites such as that of Defra for guidance on the current situation. Within the zoo community, both the BIAZA and the EAZA websites carry information about the current risk to zoo collections from bird flu. EAZA has recommended to its members that they should seek permission to vaccinate birds in their collections; BIAZA members have been provided with advice on appropriate biosecurity and veterinary surveillance measures, as well as advice on how to reduce the risk to zoo staff and to members of the public. The American Association of Zoos and Aquariums (AZA) has produced and circulated to its members detailed guidelines on the monitoring and prevention of bird flu. Another website featuring up-to-date information about AI is that of the European Food Safety Authority (EFSA); part of EFSA's role is to '*provide European risk managers with objective scientific advice on the animal health and welfare dimension of avian influenza*' (EFSA 2008).

Current EU legislation on AI is set out in EC Directive 2005/94 EEC.[22] This Directive covers areas such as monitoring and surveillance for AI in wild birds, as well as control measures to be taken in the event of an outbreak. In the UK, this EU legislation is enforced via the Avian Influenza and Influenza of Avian Origin in Mammals (England) (No 2) Order 2006 and the Avian Influenza (Vaccination) (England) Regulations 2006 (Wales and Scotland have their own versions of this legislation).

Zoo contingency plans for AI will involve consultation and discussion, decisions on appropriate control measures, and consideration of how to deal with the public perception of an outbreak affecting zoo animals.

Chytridiomycosis in amphibians

Chytridiomycosis, or chytrid[23] fungus, is the name for a fungal disease that has been strongly implicated in the decline of populations of wild amphibians around the world (Pessier 2012) (**Fig. 11.24**). The fungus or pathogenic agent *Batrachochytrium dendrobatidis* (Bd) belongs to the class Chytridiomycetes and appears to be a new genus that, until recently, had not been found in vertebrates (Crawshaw 2003). Infection causes skin problems in **anurans** (frogs and toads), ranging from cutaneous erosion to ulceration of the skin. In some species Bd infection is subclinical; in other more susceptible species, such as some tropical frogs, the disease can have a high mortality rate. The antifungal drug itraconazole and the

Figure 11.24 Wild populations of amphibians such as this White's tree frog *Litoria caerulea* appear to be particularly at risk of infection by a fungus called chytridiomycosis, or chytrid fungus. WAZA has called the current threats to wild populations of amphibians '*one of the greatest species conservation challenges in the history of humanity*'. (Photograph: Paignton Zoo Environmental Park)

---

[22] Council Directive 2005/94/EC on European Union measures for the control of avian influenza, and repealing Directive 92/40/EEC.

[23] Chytrid is pronounced 'kitrid'.

antibiotic chloramphenicol have proved effective for treating chytridiomycosis in captive animals (Pessier 2012), but these treatments are not practicable for use in the wild.

Why should a fungus that, at the moment, appears to be a problem mainly in free-living or wild amphibians be of particular concern to zoos and aquariums? In 2006, WAZA produced the following statement:

> 'Addressing the amphibian extinction crisis represents one of the greatest species conservation challenges in the history of humanity. It is clearly understood that if the global zoo community does not respond immediately and on an unprecedented scale, much of an entire vertebrate class will be lost'.

So what are zoos and aquariums doing in response to this threat to amphibians? Zippel (2005) provides a useful and comprehensive web-based review of zoo research and conservation initiatives aimed at amphibians, with links to scientific papers, zoo reports, and species information, and there is further information in **Chapter 10** (in particular, **Box 10.3**).

11.6 The diagnosis and treatment of disease in zoo animals

We have seen earlier in this chapter that diagnosis of disease is a key skill for zoo vets. Clinical signs of illness, such as a fever or rapid breathing, will rarely be specific to a particular disease. A diagnosis is usually based on a suite of characteristics, and further testing is often necessary to confirm an initial diagnosis of a particular disease. Once a disease has been diagnosed, treatment will vary, depending on whether or not the condition is **chronic**[24] and also on whether or not immediate veterinary intervention is in the animal's best interests.

11.6.1 To treat or not to treat?

Capture, restraint, and anaesthesia are all stressful procedures for animals, and particularly so for wild animals. For any given situation, the costs and benefits of treatment versus no treatment must be weighed up. It may be better to leave an animal with a superficial injury to heal on its own without treatment if the only alternative is capture and full anaesthesia. Veterinary treatment may have adverse effects on an animal's reproductive status, or may result in aggression from conspecifics when an individual is removed for treatment and then returned into a social group.

Medication that can be administered in food or drinking water may be an option when capture and injection of a drug is not desirable from a welfare perspective, or when it would put veterinary staff or keepers at high risk of injury. **Euthanasia** is also an option (this is discussed further in **Box 9.8**).

The veterinary treatment of fish poses particular challenges, and this is considered in **Box 11.5**.

11.6.2 The management of pain

The problem of assessing pain in non-human animals has been discussed in **Chapter 7**. It is widely accepted that pain has evolved because it is adaptive—that it has a protective function. Pain helps animals to distinguish between harmful and non-harmful **stimuli**, and provokes animals to avoid harmful stimuli. Pain also inhibits activities that could delay recovery—for example, by stopping an animal from moving an injured limb and so doing more harm.

It is also widely accepted that we have an ethical responsibility to reduce pain and suffering in animals in our care. Pain needs to be avoided, and when it can't be prevented it should be controlled, not only on ethical grounds, but also because pain has serious adverse physical consequences such as changes in behaviour (for example, excitability

---

[24] A **chronic** condition (when used in the context of illness) is one that persists over a long period of time and which may require long-term management (e.g. diabetes). An **acute condition** is one in which severe or aggressive illness develops, often quite rapidly.

Box 11.5 HOW DO YOU TREAT A SICK FISH?

Disease treatment for fish and other aquatic organisms in aquariums poses a number of challenges. Fish can be given drugs, such as antibiotics, and can also be anaesthetized. Drug administration is either by capture and treatment of individual fish, with the drug given orally or by injection into the coelomic cavity or into muscle, or alternatively drugs can be added to the water (immersion). Adding drugs or chemical treatments to the aquarium tank water means that all the fish and other inhabitants will be exposed; however, capture and removal of individual fish

for treatment is also challenging, particularly from large tanks. Most immersion treatments will be administered in a quarantine or isolation tank.

Some ectoparasites commonly found in aquariums can be removed by immersing saltwater fish in fresh water for a short period of time, and vice versa for freshwater fish, with a saltwater dip (Hadfield 2012). Other treatments for fish ectoparasites include copper, usually in the form of copper sulphate added to the water, although this is toxic to most aquatic invertebrates and to **elasmobranchs**, so cannot be used in tanks housing these animals.

or self-harm), muscle spasms, vomiting, and even the risk of heart damage.

The relief of pain is termed **analgesia**; drugs or treatments that reduce pain are referred to as analgesics. Some commonly used **analgesic drugs** and non-drug treatments for the relief of pain in captive animals are summarized in **Table 11.6**.

Before prescribing an analgesic, the age and condition of the animal, the apparent location and severity of the pain, whether or not the animal is in shock or dehydrated, and the possibility of any adverse reaction must be considered. Some analgesic drugs are toxic to particular animals, but safe to use in other taxa; other drugs may have

adverse side effects in pregnant mammals. The most commonly used analgesics in zoo animals are the NSAIDs, which have useful anti-inflammatory and **anti-pyretic**, as well as analgesic, properties.

Where possible, pre-emptive analgesia is preferable, because this is often more effective at controlling pain (in other words, an analgesic is administered before pain is perceived by the animal). This should always be possible for surgical procedures. More than one analgesic might be administered, from different classes of drug. Multimodal analgesia is often more effective than the administration of only one drug, or one type of drug.

Analgesic drugs for veterinary use	Other methods of pain control
Opioids, e.g. morphine	Distraction (not easy in wild animals)
Non-steroidal anti-inflammatory drugs (NSAIDs), e.g. carprofen, marketed in the UK as Rimadyl®	Application of hot or cold compresses (again, not easy in wild animals)
Alpha-2 agonists, e.g. medetomidine, marketed in the UK as Domitor®	Immobilization of fractures
Local anaesthetics, e.g. lidocaine, marketed in the UK as Lidocaine®	Transcutaneous electrical nerve stimulation (TENS)
Neuroleptoanalgesics, e.g. etorphine, marketed as M99® (these drugs are combinations of tranquillizers and analgesics, with the analgesic component being an opioid)	Acupuncture

Table 11.6 Analgesia for zoo animals

Note: This table lists only some of the more commonly used measures for relieving pain in zoo animals.

Figure 11.25 Here, a black rhinoceros *Diceros bicornis* at Ramat Gan Zoo in Israel has been darted with an anaesthetic dart prior to veterinary treatment. The animal is being supported as the drug takes effect to reduce the risk of injury as it goes down. (Photograph: Tibor Jäger, Zoological Center, Tel Aviv)

Legislation and the control of analgesic drugs

The use of analgesic drugs for animals is strictly controlled within the UK, under the Veterinary Medicines Regulations 2005; most analgesics can only be prescribed by a vet who has seen and assessed the animal.

Opioids, such as morphine, are also subject to the Misuse of Drugs Regulations 1985.

11.6.3 Anaesthesia

Anaesthesia of wild animals can be risky and stressful, both for the animal and for staff (See **Box 11.6** for a short summary of the risks to zoo staff from the use of a potentially hazardous drug, Immobilon®). There can be complications as a result of immobilization, particularly in large mammals such as elephants or rhinoceros (**Fig. 11.25**), or giraffes (see **Box 11.7**).

Box 11.6 **A SHORT NOTE ABOUT IMMOBILON®**

Immobilon® (M99™) is a powerful drug containing the opioid etorphine and acepromazine. It is used by zoos to immobilize animals such as equids and bovids. However, Immobilon® can be fatal to humans, even if it is only splashed onto the mucous membranes or onto an open wound in the skin and is not washed out immediately. This drug should only be used if the antidote (Narcan®; the generic name is naloxone) is drawn up first and an assistant is on hand to administer this in case of any accident.
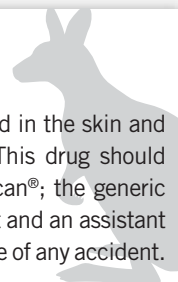
Box 11.7 THE ANAESTHESIA OF GIRAFFES

The anaesthesia of giraffes in captivity has, historically, been associated with high rates of mortality (Bush 1993; Vogelnest and Ralph 1997). Neck muscle spasms can occur as the animal recovers from the anaesthetic. Giraffes can also regurgitate and aspirate their stomach contents while anaesthetized, so fasting the animal for a period of two or three days prior to the administration of an anaesthetic is recommended by some sources (Bush 2003). This practice is controversial, however, because of the welfare implications of denying food.

To minimize the risk of complications, the head of the animal should be kept raised above the level of the stomach and the nose pointed downwards (**Fig. 11.26**). This may mean that a catwalk or other raised structure is needed for keepers and veterinary staff to access the head during immobilization. Bush (2003) suggests the use of a long board or ladder to keep the neck straight, and also suggests altering the angle of the neck every 10–15 minutes to reduce the risk of muscle spasms. Once recumbent, a blindfold and earplugs can be put in place to reduce the impact of external stimuli, such as lights and noise, and so minimize stress.

As the giraffe recovers from anaesthesia, a rope placed around the animal's shoulders can be used (Bush recommends a minimum of three people on each end of the rope) to steady the animal as it attempts to stand.

Figure 11.26 Anaesthesia of giraffes presents a considerable challenge to zoo vets. Recommendations to reduce the risk of complications include keeping the head of the animal raised above the level of its stomach (Bush 2003). Here, a team of keepers and veterinary staff at Werribee Open Range Zoo, near Melbourne in Australia, are working together to monitor and treat an anaesthetized giraffe. (Photograph: Chris Stevens, Werribee Open Range Zoo)

One of the first hurdles that a zoo must over-come before anaesthetizing an animal is to try to obtain an accurate weight, so that the correct dose of anaesthetic can be used. This is easier said than done for animals such as elephants or giraffes, but zoos can make use of industrial weigh bridges or bars (normally used for weighing heavy vehicles), and can position weigh bars under a platform set into the surface of a part of the enclosure, such as a doorway, where the animal will become accustomed to walking over it.

Ruminants can be prone to complications dur-ing anaesthesia, such as the aspiration of regurgi-tated contents from the **rumen** (the first chamber of the stomach). To reduce this risk, it is better to position an anaesthetized ruminant in **sternal recumbancy** (**Fig. 11.27**) rather than lying flat on its side, and to keep the head raised and the nose down (Flach 2003).

Figure 11.27 Sternal recumbancy in a gerenuk *Litocranius walleri* at Fort Worth Zoo in Texas, USA; the animal is lying down with the breastbone towards the ground, rather than on its side with the flanks on the ground. (Photograph: Jeroen Stevens)

11.6.4 Medication and self-medication

As Lozano (1998) has pointed out, there is now recognition that some components of diet selec-tion by wild animals are likely to have evolved to help to protect against infection by parasites, or at least to reduce the effects of parasites. As well as the active avoidance of food items and feeding areas that may be potential sources of infection by parasites, animals in the wild may seek out and eat plants and minerals (or soil) for prophy-lactic or therapeutic purposes. This is known as **self-medication** (Glander 1994).

In an experimental study of leaf-swallowing in captive chimpanzees, Huffman and Hirata (2004) found that the consumption of rough **hispid** leaves (used by wild chimpanzees to 'hook' and expel parasitic worms from the gut) was, in part, socially influenced. Some zoos are now offering their animals opportunities for self-medication by providing a range of plants, such as some herb species, that may have me-dicinal properties. (For a review of the provision of herbs and medicinal plants within primate exhibits, see Cousins (2006).)

Summary

• Zoo animal health care is a complex topic; a large zoo may keep upwards of 10,000 individual animals, from more than 500 different species, each of which will be susceptible to different diseases and health problems.

• Preventive medicine is very important for zoo animals; treating sick or injured wild animals in captivity is not easy, and it is far better to try to avoid the need for treatment in the first place.

• Diseases of concern will vary from collection to collection, depending on the species in the col-lection and local risk factors.

• Zoo staff may sometimes decide not to treat a sick or injured animal if the risks of capture and restraint appear to outweigh the possible benefits of intervention and treatment.

• Far fewer drugs and vaccines have been developed specifically for exotic animals than for farm or companion animals; zoo vets face a particular challenge in this respect.

• Zoo staff also face the challenge of sometimes having to deal with very large animals; dentistry, the treatment of an injury, and anaesthesia pose considerable problems when dealing with an animal the size of a giraffe, rhinoceros, or elephant.

Questions and discussion topics

1. In what ways does the role of a zoo vet differ from that of a livestock vet or a companion animal vet?
2. Why is preventive care of particular importance for zoo animal health?
3. Under what circumstances might zoo staff decide *not* to capture and treat a sick or injured animal?
4. What are the main bacterial diseases of concern in zoos?
5. What are the main zoonoses of concern in zoos?
6. What can be done to prevent the development of foot problems in captive elephants?

Further reading

First and foremost, Fowler and Miller's *Zoo and Wild Animal Medicine: Current Therapy* provides a wealth of practical information about the prevention, diagnosis, and treatment of disease in wild animals. This book, now in its seventh edition (Fowler and Miller 2012), is regarded by many zoo vets in the UK, the USA, Australasia, and beyond as the first point of reference for information about exotic animal diseases and medicine, and most zoo vets have at least one battered and well-thumbed copy of Fowler and Miller somewhere on their shelves. Some of the terminology used in the book will be unfamiliar to a reader without a veterinary training, because the book is written by vets

for vets, but although a glossary would be useful to the non-vet reader, it would add to the already considerable length—and weight—of this tome.

If you buy or borrow a copy of Fowler and Miller, you need to check which edition you have got hold of. The content and organization of the book varies (deliberately) quite markedly from one edition to the next; the latest edition (Fowler and Miller 2012) includes a chapter on disaster preparation for zoos and zoo vets, and an entire 'aquarium' section on aquatic animal health and medicine.

A recommended book on animal health for the general reader is Sainsbury's *Animal Health* (1998). Although this book is about livestock health and does not specifically cover zoo animal health or medicine, it is a useful and readable account of general principles of health care for captive animals. There are sections on metabolic diseases and on different types of disease, as well as very clear tables listing diseases (including zoonoses) in livestock. Another accessible book for non-vets is Bowden and Masters' *Textbook of Veterinary Medical Nursing* (2003). For the non-vet who wants a clear and easy to read account of veterinary diagnostic procedures, or an introduction to infectious diseases, this book is excellent. As with Sainsbury's book, this text is not aimed at zoo staff, but nevertheless there is much useful general information about veterinary medicine.

Kleiman *et al.*'s *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2010) has a number of chapters which touch on health issues, such as a summary of emerging and zoonotic diseases, and a review of the management of pregnancy and parturition in captive mammals. Stephen Jackson's *Australian Mammals: Biology and Captive Management* (Jackson 2010) provides a section on health requirements for each taxonomic group considered in the book.

For further information about zoo animal dentistry, Glatt *et al.* (2008) provide a useful review in the *International Zoo Yearbook* of dental problems and treatment in zoo animals, based on a survey of AZA member zoos. The textbook *A Colour Atlas of Veterinary Dentistry and Oral Surgery* (Kertesz 1993) is one of only a small number of books that look in any detail at veterinary dentistry for wild animals. There is also a chapter on oral disease and dentistry in exotic animals in *Veterinary*

Dentistry: Principles and Practice (Wiggs and Lobprise 1997).

Websites and other resources

For zoos within the UK (and, indeed, further afield), there is a wealth of useful information about animal health care on the Defra website (**http://www.defra.gov.uk**). This includes guidelines on current legislation, as well as information on topics such as notifiable diseases and updates on the current situation with regard to outbreaks of avian influenza (AI) in wild birds. Chapter 5 of the *Zoos Expert Committee Handbook* (Defra 2012b), which is published online, is a good place to start.

The websites of BIAZA (**http://www.biaza.org.uk**) and EAZA (**http://www.eaza.org**) are another useful source of information about animal health issues relating to zoos. For zoos in North America, the websites of both AZA (**http://www.aza.org**) and the AAZV (**http://www.aazv.org**) provide information about zoo animal health care and related issues such as quarantine regulations, with links to various guidelines and reports. Information about a wide range of animal health issues in Australia, and particularly about infectious disease, can be found on the AHA website (**http://www.animalhealthaustralia.com.au/**). A comprehensive online resource is provided by the Wildlife Information Network (WIN). Its searchable online encyclopaedia is called Wildpro® and contains many useful links to information about animal health.

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.
http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Chapter 12
Feeding and nutrition

For those of us whose experience of feeding animals comprises a trip to the supermarket to buy a pack of dog or cat food, feeding zoo animals probably appears relatively straightforward. This is far from the case, however. In the first place, it is by no means clear for a lot of animals exactly what foods we should be giving them, because our knowledge of their natural diets is often quite poor. But even if we know what animals usually eat in the wild, it is unlikely that the zoo will be able to duplicate their natural diet. This is either because of unavailability of the required items, or because it is simply not feasible—or, in some cases such as live vertebrate prey, even legal (in the UK[1])—to supply food to animals in the form that they eat it in the wild.

These difficulties can be overcome largely by aiming to provide zoo animals with the levels of **nutrients** that they would get in the wild, rather than trying to recreate the wild diet exactly (Dierenfeld 1997a). This is important, because **nutrition** can have profound effects on other aspects of an animal's life history, such as physical and mental development, reproduction, mortality, and emotions, as well as its basic health.

But there is more to this than feeding. Many animals in the wild spend a great deal of time seeking out and processing food, and giving animals the opportunity to do similar things in captivity is an important part of zoo husbandry.

In this chapter, we will consider the following topics.

Before we can look at how zoos can best meet the nutritional needs of their animals, we need to know something about how different types of animal obtain their food and also about essential nutrients in the diet. Therefore the first two sections of this chapter provide a brief overview of feeding ecology and general nutritional theory. If you are already familiar with the terms **carnivore**, **herbivore**, **ruminant**, etc., and have a good basic knowledge of the anatomy and function of the digestive tract, then you may

[1] Feeding live vetebrates to zoo animals in the UK is not recommended in the formal government guidance to zoos in the UK (see the Secretary of State's Standards of Modern Zoo Practice (Defra 2012a)). Although similar specific legislation does not exist in other countries, in practice relatively few zoos globally feed live vertebrate prey. Some do feed live fish.

wish to skip **sections 12.1** and **12.2**, and go straight to the practical information about formulating diets for zoo animals, from **section 12.3** onwards.

Special topics, such as a brief history of zoo animal diets and nutrition, are included in boxes throughout this chapter. For example, **Box 12.5** looks at why keepers chop up food for zoo animals, when wild animals manage perfectly well without having their food chopped up for them; other boxes provide information about plant chemical defences against herbivory (**Box 12.1**) and on some recommended sources of detailed information on the nutrient requirements for different species (**Box 12.3**).

12.1 Feeding ecology

Wild-living animals have to find food, process it, and eat it. They have to do these things in an environment within which other organisms live: some of these organisms will be potential food items; some will be competitors looking for the same food; some will be predators looking to make a meal of them; and some will be of no food relevance whatsoever. Evolution has equipped these animals with morphological, physiological, and behavioural adaptations for dealing with these eventualities, and although many zoo animals have been removed from this ecological context, it is important that we know something about these adaptations so that they are satisfied as much as they can be by feeding regimes in the zoo.

12.1.1 Feeding categories

Various different terms are used to describe the sorts of food that animals eat. The most familiar are the very broad terms 'carnivore',[2] to describe an animal that feeds on other animals, 'herbivore' describes an animal that feeds on plants, and **omnivore** describes an animal that eats both plant and animal food. These terms are so broad that they are not always particularly useful, so some narrower terms are also used to describe more specialized diets within these categories.

Thus, a carnivore that eats fish is referred to as a 'piscivore', while one that eats terrestrial arthropods is called an 'insectivore'. Herbivorous species might eat fruit (a 'frugivore') or leaves (a 'folivore') (**Fig. 12.1**).

This sort of naming of categories can go on apparently endlessly. Animals such as galagos (bushbabies) and marmosets, which include a quantity of plant exudates in their diet, are now often referred to as 'gummivores' (for example, Huber and Lewis (2011) assess enrichment for 'captive gummivorous primates'); animals such as the leatherback

Figure 12.1 The koala bear *Phascolarctus cinereus* is an example of a folivore—that is, a specialist herbivore that feeds on leaves. The diet of the koala bear is made up largely of eucalyptus leaves. (Photograph: Ben Gibson)

[2] The term 'carnivore', meaning an animal that eats other animals, is easily confused with the taxonomic term Carnivora. The name Carnivora refers to an order of mammals that includes meat-eating animals such as lions and tigers, but also plant-eating giant pandas and omnivorous badgers. Note the lower- or upper-case initial letter 'c' or 'C'; this is the key difference. So a tarantula spider, or a shark, or a snake is a carnivore, but not a Carnivore.

turtle *Dermochelys coriacea*, which consume jelly-fish, are 'medusivores' (e.g. Pierce 2005).

With a few caveats, terms such as 'carnivore' and 'herbivore' apply across all animal **taxa**. In the literature on avian nutrition (see, for example, Klasing's 1998 book, *Comparative Avian Nutrition*), the term 'granivore' occurs quite widely, not necessarily because there are a very large number of species of granivorous, or grain-eating, birds, but because the **nutritional requirements**[3] of commercially important granivores such as the chicken *Gallus domesticus* and the Japanese quail *Coturnix japonica* have been extensively studied.

Specialist and generalist feeders

What does become clear from this naming of categories is that some species have much broader diets than others. Thus, we can think in terms of feeding specialists, who take a very narrow range of food items, and generalists, who take a very broad range. These terms should be thought of in a relative, rather than an absolute, sense. For example, lions *Panthera leo* preferentially prey on species within a weight range of 190–550 kg, with a preference for prey of about 350 kg (Hayward and Kerley 2005). In this respect, they are specialists, but they are more generalist than pandas (both giant and red), which feed on bamboo (Gittleman 1994; Wei *et al.* 1999). In the same way, lions are also more specialist than red foxes *Vulpes vulpes*, which eat scavenged food, birds, small mammals, earthworms, other invertebrates, and fruit (Doncaster *et al.*1990).

Feeding methods

It is also possible to categorize animals according to the way in which they obtain their food. For example, some animals filter small food particles that are in suspension in water and thus are

Figure 12.2 This photograph shows a Chilean flamingo *Phoenicopterus chilensis*, a vertebrate filter feeder. There are many invertebrate examples of filter feeders, but relatively few vertebrates feed in this way. (Photograph: Sheila Pankhurst)

known as suspension, or filter, feeders. In the zoo, such feeders are most likely to be seen in the aquarium (sponges, **lamellibranchs**, and other aquatic invertebrates), but some vertebrates, notably flamingos, also feed this way (**Fig. 12.2**).

Carnivorous species are often predators, which hunt, trap, or ambush their prey, but they may also feed on material that somebody else has caught, or that they find dead (scavengers), or may even steal it from someone else (kleptoparasites). Herbivorous species may eat from the ground layer of plants (grazers), or from bushes and trees (browsers). In all of these cases, the different animals have evolved morphological specialisms, usually in and around the mouth (different teeth, different beak forms,[4] etc.) or front limbs (claws,

---

[3] The terms **nutritional requirements** and **nutritional needs** are often used interchangeably, but in some texts at least there is a difference in meaning. The term 'nutritional requirements' usually refers to a set of quite specific requirements that have been quantitatively and qualitatively measured, for example in the publications on nutrient requirements of livestock by the National Research Council (NRC) in the USA. The term 'nutritional needs' is often used in a broader sense and does not necessarily imply that a detailed analysis has taken place.

[4] Klasing (1998) provides an extensive list of the different ways in which birds obtain their food, from dabblers (such as many duck species) and excavators (such as woodpeckers) to probers (such as the curlew *Numenius arquata*), which insert their bill into a substrate, such as mud or sand, to obtain prey.
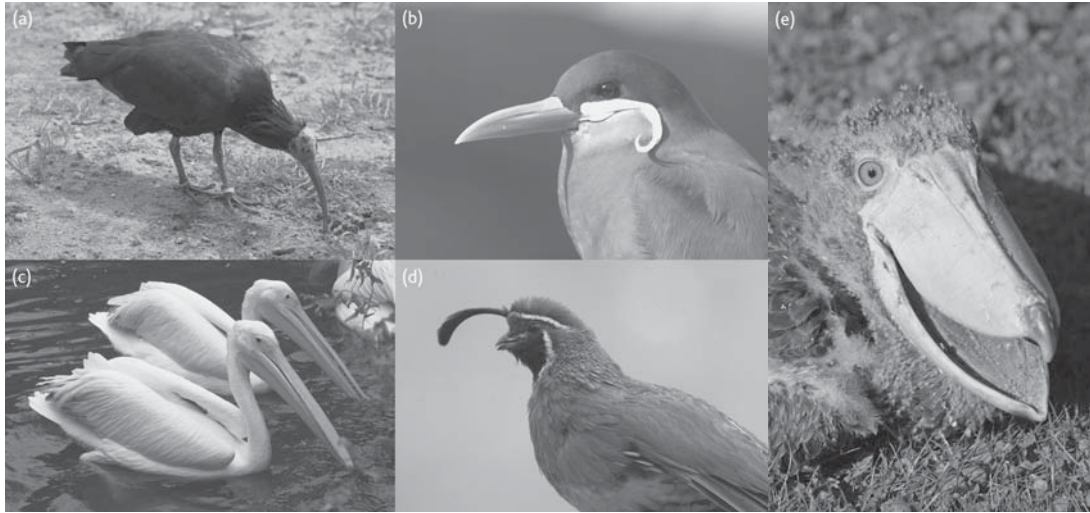
Figure 12.3 Birds show many different specialized beak shapes, such as (a) the probing bill of the Waldrapp or northern bald ibis *Geronticus eremita*, (b) the stabbing bill of the fish-eating Inca tern *Larosterna inca*, (c) the very large pouched beak of the Eastern white pelican *Pelecanus onocrotalus*, adapted for catching and storing fish, (d) the small beak of the desert-living Gambel's quail *Callipepla gambelii*, adapted for feeding on seeds, and (e) the extraordinary beak of the shoebill or shoe-billed stork *Balaeniceps rex,* which, with its extensive gape and sharp edges, is adapted to taking large prey such as fish, amphibians and reptiles such as frogs and lizards, and even waterfowl and small mammals. (Photographs: (a)–(d) Sheila Pankhurst; (e) Jeroen Stevens)

grasping fingers, etc.) for processing the food (e.g. biting, tearing, grinding, etc.) before it is swallowed (**Fig. 12.3**).

12.1.2 Gastrointestinal tract anatomy and function

All vertebrate animals have a gastrointestinal (GI) tract or digestive tract, with associated organs and glands that release enzymes and other substances into the gut (Stevens and Hume 1995; McDonald *et al.* 2011). But there is considerable variation between, and even within, taxa in the morphology of the GI tract, depending on whether an animal is a carnivore or a herbivore and how it obtains its food. Not all structural elements of the vertebrate GI tract are found in all species. Stevens and Hume (1995) suggest that comparisons between the digestive tracts of different taxa are best made

under broad functional headings such as 'foregut', 'midgut', and 'hindgut'[5] (also reflecting the embryological origin of the different parts of the digestive tract).

Not all invertebrate animals have a gut, but, for those that do, there are functional similarities with the vertebrate gut. A cricket or locust, for example, has a tubular gut with a crop, in which food can be stored temporarily, and a gizzard, in which food is ground up. Insects also have an intestine (in which nutrient absorption occurs) and an anus. However, the overwhelming majority of zoo animals are vertebrates and so the remainder of this section is about the vertebrate gut.

In its simplest form, the vertebrate GI tract is a long tube with a bulge, the stomach, at one end (some fish do not have a proper stomach). Although simple in structure, the midgut and

---

[5] The terms 'small intestine' and 'large intestine' can be misleading, because these sections of the GI tract may be almost the same diameter in some vertebrate species (Stevens and Hume 1995). The terms 'midgut' and 'hindgut' distinguish between these sections on the basis of their main function.

hindgut of the omnivorous American black bear *Ursus americanus* (**Fig. 12.4**) combine to make a relatively long intestinal tube between the stomach and the anus. In general, carnivores have a short simple GI tract and herbivores have a much longer GI tract, with the ruminant herbivores possessing the most complex digestive system (**Fig. 12.5**) (we shall return to the ruminant digestive system later in this chapter).

What are the reasons for these differences between carnivores and herbivores in the structure and length of the GI tract? To answer this question, we need to look at the process of **digestion** and, in particular, the problem that herbivores face in breaking down the tough material that makes up plant cell walls.[6]

Digestion

The macromolecules that animals ingest as food are broken down into smaller molecules in the process of digestion. This breakdown of food during digestion takes place by means of
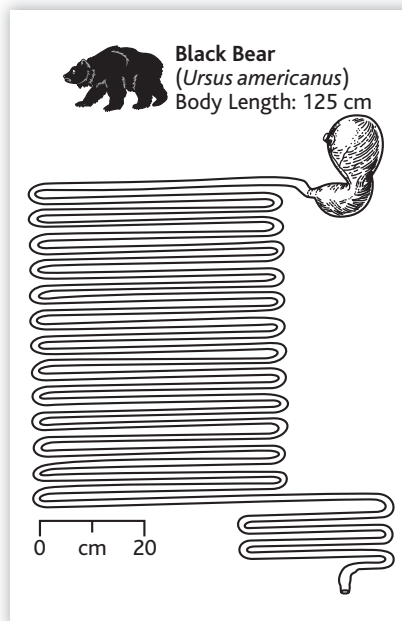
Figure 12.4 This diagram shows the relatively simple gastrointestinal tract of an omnivore, the American black bear *Ursus americanus*. (Reproduced with permission from Stevens and Hume (1995))
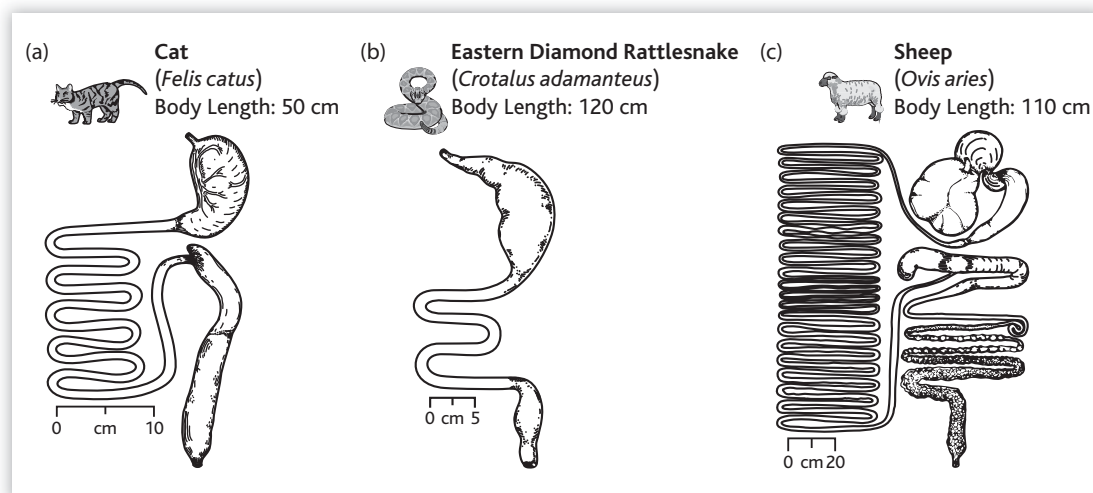
Figure 12.5 These diagrams show the gastrointestinal tracts of (a) a domestic cat *Felis catus*, (b) a reptilian carnivore, the eastern diamond rattlesnake *Crotalus adamanteus*, and (c) a sheep *Ovis aries*. The carnivorous cat and snake have a much shorter and simpler GI tract than the sheep, which is a ruminant herbivore. ((a) and (b) reproduced with permission from Stevens and Hume (1995)); (c) reproduced with permission from Stevens (1977))

---

[6] The cell walls of fruits are not as tough as those of leaves, stems, and other plant material, and are easier to break down with enzymes during digestion. Thus, frugivores face less of a challenge digesting plant material than browsers or grazers.

enzymatic hydrolysis reactions, in which water in the presence of a digestive enzyme splits apart larger molecules. The smaller molecules can then be absorbed and utilized for energy, growth, and tissue repair.

A lot is known about the mechanical and chemical processes involved in digestion, as well as the neural and endocrine mechanisms by which these are regulated. These topics are outside the scope of this book, however, so you are referred to good animal physiology textbooks such as Schmidt-Nielsen (1997) and Willmer *et al.* (2004). But it is appropriate at this stage to look briefly at the problems involved in **cellulose** digestion.

The problem of cellulose

Cellulose is a carbohydrate macromolecule used extensively by plants in their structure (for example, as cell walls) and, because of this, is potentially one of the most widely available sources of energy for animals. But, for some reason, very few animals have evolved an enzyme (a cellulase) for digesting cellulose, so how do they survive on a diet of plant material?

The answer, for many herbivorous animals, is that they rely on **symbiotic** micro-organisms living in their digestive tract. These micro-organisms could not survive independently outside the animal's body and the animal could not derive energy from plant material through its own digestive processes.

The general name for the micro-organisms that inhabit the digestive tract is the **gut microflora**.[7] These micro-organisms can digest cellulose to produce not simple sugars (which would be the case in starch digestion), but volatile fatty acids, a process often referred to as fermentation. Examples of gut fermentation to process tough plant materials in the diet can be found throughout the vertebrates. For example, animals as diverse as the llama *Llama glama*, the green iguana

Figure 12.6 The green iguana *Iguana iguana* is an example of a gut fermenter—an animal that uses microbial fermentation in the gut to break down ingested plant material. (Photograph: Christian Mehlführer/CC-BY)

Iguana iguana (**Fig. 12.6**), and the green sea turtle *Chelonia mydas* use microbial fermentation of plant foods, as do many **gallinaceous** birds.

Probably the most complex, but efficient, evolutionary outcome of this symbiotic relationship is seen in the ruminant mammals (animals that chew the cud). These mammals are all members of the order Artiodactyla[8] (one of the orders of **ungulates**, or hoofed mammals) and most are members of the sub-order Ruminantia; the camels and llamas are an exception, and belong to the family Camelidae, within the sub-order Tylopoda (Macdonald 2009).

The ruminant stomach

In ruminants, the stomach has become more complex by the addition of extra chambers (**Fig. 12.7**), one of which, the **rumen**, is particularly large and houses a substantial microbial population (non-ruminant animals with a single-chambered stomach are sometimes referred to as **monogastric** animals—for example, bears, rodents, pigs, and humans). These micro-organisms live in what is essentially a fermentation vat, kept at a temperature of around 37–40°C and buffered

---

[7] All animals have a gut microflora, but there is considerable variation in the extent to which different taxa rely on gut fermentation for their supply of energy and nutrients.

[8] Mammalian taxonomy is still undergoing rapid change, with new insights from molecular analysis overturning traditional views on how animals should be grouped (see, for example, Perelman *et al.* (2011) on the molecular phylogeny of living primate species).
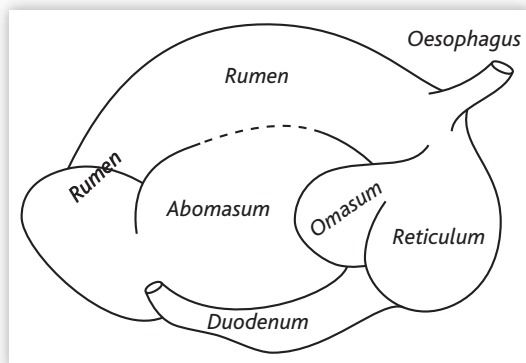
Figure 12.7 This diagram shows the basic structure of the chambered stomach of a typical ruminant. One of the stomach chambers, the rumen, is a major site for microbial fermentation of plant material. (Picture: Geoff Hosey)

from pH fluctuations by the host animal's saliva, which contains large quantities of sodium bicarbonate in solution.

Ruminants often feed very rapidly and swallow their food in a relatively unchewed state. When the rumen is nearly full, the animal rests and starts ruminating, which is a process of bringing the unchewed food back to the mouth for more chewing ('chewing the cud'). When this chewed food is swallowed, it sinks to the bottom of the rumen, where it is broken down to volatile fatty acids (mostly acetic, propionic, and butyric acids) by the rumen microflora.

Importantly, the microflora also synthesize amino acids and vitamin B group compounds (see **section 12.2.2**), which are available for the host animal's use. Because of this, the ruminant gets more from its microflora than just the breakdown products of cellulose.

Foregut and hindgut fermenters

A useful way of considering the nutritional requirements and digestive capabilities of herbivorous animals that rely on gut fermentation is to distinguish between 'foregut fermenters' and 'hindgut fermenters'—in other words, to consider where, within the gut, there is space for fermentation[9]. In ruminants, this space is the rumen, which is part of the stomach and so within the foregut (the foregut can be defined, very roughly, as the portion of the gut from the mouth to the stomach exit). Among non-ruminant mammals, sloths, langur monkeys, and kangaroos also have large stomachs with several compartments in which microbial fermentation of cellulose takes place, so these animals are also foregut fermenters.

In other mammals (particularly rodents, lagomorphs, and equids), caecal fermentation takes place: the ingested plant material travels through the alimentary canal, as it does in other mammals, but when it reaches the **caecum**, it is digested by the micro-organisms living there. So these animals, along with the non-mammalian herbivores that make use of caecal fermentation (we have already mentioned the green iguana and the gallinaceous birds as examples), can be grouped together as hindgut fermenters.

The location within the herbivore gut of the major site for fermentation of plant materials has important implications for the absorption of nutrients (Oftedal *et al.*1996). A substantial proportion of the absorption of nutrients takes place in the midgut, so hindgut fermenters appear to be at something of a disadvantage, in that the breakdown of cellulose occurs *after* the ingested food material has passed through the main absorptive area of their digestive tract. In a number of taxa, some herbivores (for example, many lagomorph and rodent species) that have caecal fermentation also reingest their faeces to extract some of these products a second time around. This strategy, called **coprophagy**,[10] allows better overall absorption of the products of digestion and can play

---

[9] Some authors refer to ruminants as pregastric fermenters, and to hindgut fermenters as postgastric fermenters.

[10] Coprophagy, or faeces eating, is by no means confined to lagomorphs and rodents, or indeed to mammals. There have been reports of coprophagy in mammals ranging from koalas (Osawa *et al.* 1993) to ringtailed lemurs *Lemur catta* (Fish *et al.* 2007), and in non-mammalian species such as coral reef fish (Robertson 1982), hatchling green iguanas (Troyer 1984a; 1984b), and even one species of cave-dwelling salamander (Fenolio *et al.* 2006).

a very important role in the nutrition of species such as rabbits.

Given that foregut fermentation allows absorption of nutrients in the midgut without the need for strategies such as coprophagy to improve the efficiency of nutrient uptake, why are so many animals hindgut or caecum fermenters? Rumination is highly efficient, but it carries a cost in terms of the time that it takes for food to pass through the GI tract. For a very large herbivore, such as a horse, a rhinoceros, or an elephant, the best strategy is a high intake and the faster throughput that can be achieved with a simpler digestive tract.

This gives the greatest net intake of nutrients, despite the lower efficiency of hindgut fermentation (Macdonald 2009).

A consequence of the difference between these two feeding strategies (**Fig. 12.8**) is that rumination is only effective for animals in a certain size range. The largest ruminant is the giraffe, at up to about 1,200 kg body weight, but the largest hindgut fermenters can weigh several tonnes (for example, a rhinoceros can weigh more than 2 tonnes and a large male African elephant *Loxodonta africana* more than 6 tonnes).
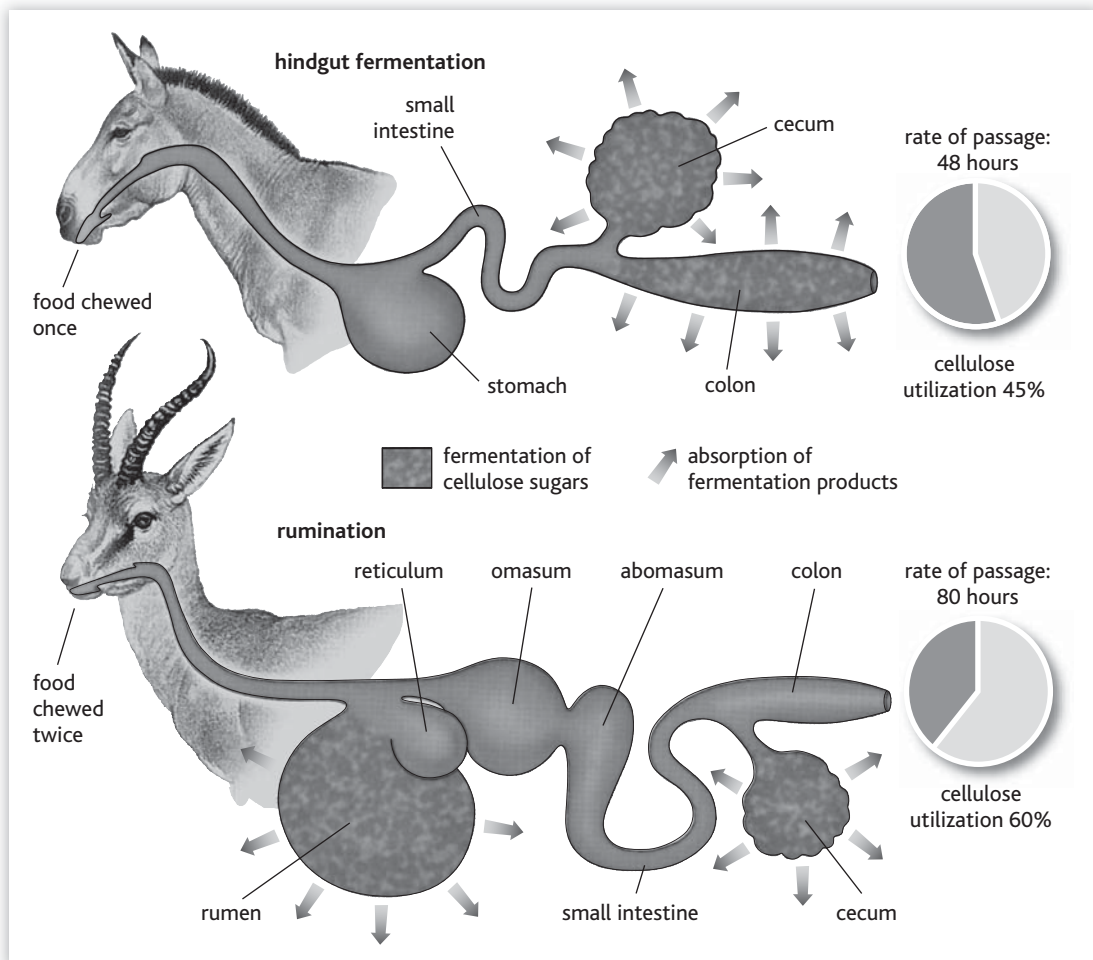
Figure 12.8 Ungulates have different strategies for digesting cellulose. Equids, such as Przewalski's horse *Equus ferus przewalskii*, have a faster gut throughput, but lower rate of cellulose utilization, whereas ruminants, such as gazelles, have greater digestive efficiency, but a slower throughput of food. (Reproduced with permission from Macdonald 2001)

12.1.3 Food selection: do animals have 'nutritional wisdom'?

Of course, knowing that a species is a herbivore or carnivore, or even what type of herbivore or carnivore, does not always help us very much when formulating diets for these animals in captivity. Both specialists and generalists do not usually simply eat everything that they come across that happens to be within the broad category of 'browse' or 'fruit', or whatever else they are adapted to eat. Most animals are very selective about what they eat and will seek out, or choose, particular preferred food items,[11] while rejecting others that might seem to us to be perfectly acceptable.

The task that animals have in the wild is to satisfy all their nutritional requirements. At the cellular level, however, the requirements of most animals, whatever their species, are pretty much the same (Moore *et al.* 2005). The differences that we see in food selection reflect different evolutionary strategies for getting those nutrients.

How do animals choose their diets?

It is possible that animals have an innate **nutritional wisdom** that allows them to select a balanced diet by detecting the nutritional quality of the different foods they encounter; this hypothesis is termed **euphagia** (Moore *et al.* 2005). But most evidence of animal food selection contradicts this view; for example, captive capuchin monkeys *Cebus apella* choose a variety of different foods in preference to **monkey chow**, even though the chow has high energy and is designed to provide a complete and balanced diet for monkeys (Addessi *et al.* 2005). Even to us, monkey chow does not look particularly enticing, so we could perhaps suggest that palatability is an important component of diet selection. But what does palatability tell the animal about the food?

One possibility, termed the 'hedyphagia hypothesis' (Moore *et al.* 2005), is that animals have evolved to find nutritious foods nice tasting and poor-quality or toxic foods unpleasant tasting. While this idea has some intuitive appeal, there is little evidence to support the notion that animals have an innate ability to detect high-quality nutrients in their food through sensory cues (Moore *et al.* 2005). For example, food selection trials with blue duikers *Cephalophus monticola* and white-bellied duikers *C.leucogaster* showed that the animals selected natural foods on the basis of colour over and above features such as size, shape, or chemical composition (Molloy and Hart 2002).

A major problem with both the euphagia and hedyphagia hypotheses is that, by seeing food selection as an innate ability, we cannot account for the flexibility that animals show when they encounter novel foods, or when they experience adverse effects (such as nausea) after eating something. All the evidence suggests that **learning** plays a large part in the development of an animal's food preferences and aversions, whether in the wild or in captivity, and helps to explain why many herbivores seek out variety even if nutritional needs can be met by a less varied diet (Provenza 1996).

Plant defences against herbivory

Plants are not passive participants in the process of herbivory.[12] It is not always in their best interests to be eaten by an animal, so many plants have evolved structures and chemicals to deter animals from eating them. These structures might include things such as spines and thorns. Less obvious are chemical defences, which include a variety of **plant secondary metabolites (PSMs)**,[13]

---

[11] The processing of food takes time and energy, so animals must take account of this in their decisions about whether or not to eat certain items. But the use of the word 'decisions' should not be taken to imply conscious or deliberate choice; animals have evolved to make decisions about foraging and other behaviours on the basis of what might be thought of as simple 'rules of thumb'—that is, the product of innate behaviours and learning—without necessarily any need for conscious action.

[12] Sometimes, it is in a plant's interests to be eaten—for example, when seeds need dispersing by animals, or need to be digested by an animal in order to start the germination process.

[13] One of the best-known plant secondary metabolites is nicotine, found in tobacco plants.

substances that are so-called because they are synthesized from the products of ordinary or primary metabolism. These substances act to make plants distasteful or even toxic, or may make it difficult for the animal to extract the important nutrients.

PSMs are so ubiquitous that herbivores in the wild cannot feasibly avoid them (Moore *et al.* 2005), and nor can zoos entirely avoid feeding **forage** or browse containing PSMs. So the objectives for zoos are to understand which PSMs may be found in the forage and browse that they feed to their animals, what the effects of these substances may be, and also to keep the amounts of PSMs in the diet of their herbivores within safe limits. Further information about PSMs is provided in **Box 12.1**.

Box 12.1 THE PLANTS FIGHT BACK

Most of the plant chemical defence substances referred to as plant secondary metabolites (PSMs) belong to one of three categories (Harbone 1991): phenolics (e.g. anthocyanins and tannins); nitrogen-containing compounds (such as alkaloids); and terpenoids (or isoprenoids). Tannins, for example, are found in varying amounts in almost all plant species worldwide, with browse containing greater amounts than grasses. Oak bark and acorns—and, to a lesser extent, oak leaves—are particularly rich sources of tannins.

Often, these substances are bitter-tasting, which acts to deter animals from eating them; indeed, some plants advertise their presence in, for example, bitter-tasting secretions that are released when the plant's tissue is damaged. Many herbivores are able to break these compounds down (detoxification), so they are able to tolerate feeding on the plants provided that their intake remains below a certain threshold. The speed at which herbivorous mammals can detoxify these compounds is size-related, with smaller species able to detoxify more rapidly than larger species. But metabolic requirement per unit of body mass decreases as body mass increases, so small mammals ingest larger doses of PSMs per unit of body mass than do larger mammals in order to meet their metabolic requirements (Freeland 1991).

In the UK, in order to address the challenge of which browse could safely be fed to zoo animals (**Fig. 12.9**), researchers at Paignton Zoo Environmental Park set up a browse database (Plowman and Turner 2001b; 2006) after surveying keepers at a number of zoos to find out which browse species they were using. Perhaps not surprisingly, wildlife parks with extensive grounds fed a greater variety and amount of browse to their animals. The browse species most commonly fed to zoo animals, among the zoos that responded to the survey, were willow *Salix* spp. Very few cases of poisoning or other ill effects were reported.

Copies of the browse database, on CD, are available from BIAZA and can be ordered for a small charge via the BIAZA website. The Dutch and Belgian Zookeepers Federation, De Harpij, has produced a Browse Identification Book (2012), covering similar ground (and with very good illustrations). See **Further reading** at the end of this chapter.

Figure 12.9 Giraffes *Giraffa camelopardalis* are browsers. At Colchester Zoo in Essex, members of the public can feed the giraffes with browse supplied by the zoo, during an educational presentation about the diet and nutrition of this species. (Photograph: Sheila Pankhurst)

12.2 Basic nutritional theory

Why do animals need food anyway? All living things require energy to operate their cellular and metabolic machinery, and also to fulfil their life history activities, including growth and reproduction. For animals, that energy is obtained by consuming plants (**Fig. 12.10**) or other animals. The correct term for this is 'heterotrophic',[14] which means an organism that obtains carbon for growth from consuming **organic**[15] matter (plants, by contrast, can derive their carbon and energy from non-organic sources, and are referred to as 'autotrophic').

The compounds which supply that energy are mostly carbohydrates and fats, although energy can also be derived from proteins.

In general, animals have no specific requirements for any particular carbohydrates, fats, or proteins; just about any will do equally well. However, there are certain specific substances, both organic molecules and chemical elements, that are essential, in the sense that the animal must have a supply of them in its diet, usually because they are a necessary component of enzyme systems and, even if they are organic, the animal may not be able to synthesize them itself. Thus, animals may have specific nutritional requirements over and above the basic need for a supply of energy.

12.2.1 Energy and metabolism

Energy is required by animals to operate their physiological processes, to be active and behave, and to grow and reproduce. Energy enters the animal's body as food and, in its use for physiological and behavioural processes, it is lost again from the body. Some energy is also lost in urine (**Fig. 12.11**), and some more (which has never been assimilated) in faeces.

If food intake exceeds the amount of energy used, the surplus is stored, usually as fat. Conversely, if food intake is less than the amount of energy consumed, stored energy is liberated by metabolizing those fats. We can, then, think of the

Figure 12.10 Squirrel monkeys, such as this free-ranging black-capped squirrel monkey *Saimiri boliviensis* at Apenheul Primate Park in the Netherlands, feed on fruits, flowers, and insects, which they obtain while foraging among vegetation. (Photograph: Sheila Pankhurst)
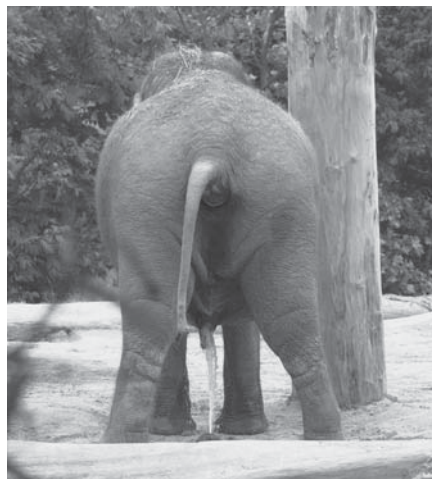
Figure 12.11 An Asian elephant *Elephas maximus* at Rotterdam Zoo in the Netherlands: some energy is lost from the body during urination. (Photograph: Sheila Pankhurst)

[14] Heterotrophic organisms are those that cannot synthesize their own food and need to take in and break down complex organic substances for nutrition (either by eating plants or by eating other animals). Plants and algae are autotrophic; they derive their carbon and energy from non-organic sources (water and carbon dioxide).

[15] The term **organic** refers to carbon-based compounds, which usually also contain oxygen and hydrogen. These compounds are not necessarily the result of living processes.

animal as a system through which energy flows (**Fig. 12.12**). The values can, in principle, be measured and they all come together in an equation that represents the energy budget of the animal:

$$C = P + R + U + F$$

(**Fig. 12.12** for definitions.)

In this budget, P represents any energy that the animal has available to put into growth. If the value of this is zero, then the animal can be said to be on **maintenance rations**—the amount of energy entering the animal is equal to the amount leaving the animal. **Figure 12.12** also shows A, or assimilated energy. This is, effectively, that part of the ingested energy that the animal has available for its use. Values of A can vary widely according to the kind of food that the animal is eating. Thus, herbivores, for example, usually have a low A:C ratio (about 57 per cent, meaning that only just over half of the energy in their food is being assimilated) because cellulose, from which plant cell walls are made, is difficult to digest (see **section 12.1.2**). Because animal material does not contain cellulose, carnivores, on the other hand, assimilate about 80 per cent of the energy in their food, even without such long or complex digestive tracts as herbivores.

The rate at which animals use energy can be broadly referred to as their **metabolic rate**, which is energy metabolism per unit time. Strictly, this should be measured as the **basal metabolic rate** (which is, effectively, the minimum amount of energy usage required to support life processes), but measuring this in most animals is not feasible, because it has to be done in very particular conditions. Instead, most animal measurements are of the standard metabolic rate, which is the resting or fasting metabolism at a given temperature. If we measure the overall metabolic rates of a range of animals, we find that large animals have higher metabolic rates than smaller animals, but if we standardize metabolic rates per unit mass of the animals, in fact, we can see that smaller animals have a greater metabolic rate per unit mass than larger animals. An understanding of metabolic rate—or at least a basic knowledge of where to find this information—is important in formulating diets for zoo animals; zoos need to know how much to feed, as well as which nutrients should be present in the diet.

12.2.2 Specific nutritional requirements

Nutritional requirements are the particular elements or compounds that an animal must have in its diet in order to satisfy all its requirements for growth and for building and maintaining its metabolic machinery. The first group of these essential substances is made up of organic compounds such as vitamins and amino acids. The second group comprises particular elements, which may be required in quite substantial quantities (or, in most cases, in just tiny amounts), such as many minerals.

Essential organic compounds

Proteins are important constituents of animal bodies because they form much of the body's structure, but also because enzymes and some other compounds involved in physiological processes (for example, some hormones) are also proteins. Animals construct their own proteins from the amino acids that they obtain by digestion of plant or animal proteins in their diet.

Animals are able to synthesize about half of the twenty common amino acids that make up most proteins from other amino acids. These are termed 'non-essential amino acids', not because
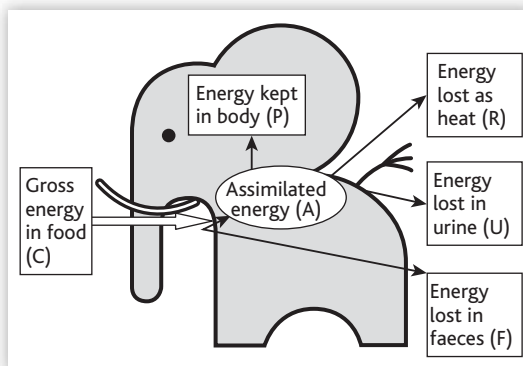
Figure 12.12 This diagram shows energy flow through a typical vertebrate animal. The equation C = P + R + U + F represents the energy budget of the animal. (Picture: Geoff Hosey)

they are not important, but because they do not have to be present in the diet. In contrast, the other amino acids are essential, meaning that animals cannot synthesize them and therefore must ingest them as part of their food.

Similarly, there are essential fatty acids (EFAs) which must be present in the diet of mammals (mammals cannot synthesize these substances). Nowadays, fatty acids are often referred to as belonging to one of two main categories: saturated and unsaturated. The unsaturated fatty acids can be further divided into monounsaturated and polyunsaturated fatty acids, and it is in this last category that we find the so-called essential fatty acids, which are alpha-linolenic acid (often represented as 'α-linolenic acid') and linoleic acid[16] (McDonald *et al.* 2011). In the diet, the so-called oilseeds, such as linseed or rapeseed oil, are particularly good sources of alpha-linolenic acid. Alpha-linolenic acid is also found in fish oils (which is the main reason why we are encouraged to include oily fish, such as salmon or mackerel, in our diet).[17]

Vitamins

Vitamins and related compounds are organic compounds that are only required in small amounts, but which fulfil important metabolic roles within the body, often as coenzymes (McDowell 2000). Some vitamins (most famously, perhaps, vitamin C, a lack of which causes scurvy[18]) are well known to us because of the dramatic effects that their absence in the diet can cause in human bodies, but, again, we know less about how they are significant to other species. Vitamins were only discovered and isolated in the twentieth century, and the concept of deficiency diseases due to a lack of a specific vitamin in the diet is relatively new, although the diseases themselves (such as scurvy and beri-beri) have been known for much longer.

Figure 12.13 Teleost (bony) fish, such as this catfish at Warsaw Zoo, are unable to synthesize vitamin C and so must obtain this nutrient from dietary sources. Other animals that are unable to synthesize vitamin C are primates, some fruit-eating bats, guinea pigs, and many invertebrates. (Photograph: Barbara Zaleweska, Warsaw Zoo)

Chemically, the vitamins are a diverse group. Some animals are able to synthesize some vitamins for themselves; others must be present in the diet. For example, amphibians, reptiles, most birds, and most mammals can synthesize vitamin C (ascorbic acid), but primates, some fruit-eating bats, guinea pigs, **teleost** fish, and many invertebrates cannot (McDowell 2000) (**Fig. 12.13**). Similarly, ruminant mammals have no dietary need for some of the B-group vitamins, because these are synthesized by the microbial flora living in the rumen.

Vitamins are often categorized as water-soluble or fat-soluble. An excess of a water-soluble vitamin, such as vitamin C, will simply be excreted. However, fat-soluble vitamins (A, D, E, and K), will be stored in body fat and can sometimes build up to toxic levels in the liver if ingested in excess.

Vitamin D is essential in the body of vertebrates for the absorption and metabolism of calcium (for this reason, it is also called 'calciferol'). This fat-soluble vitamin is unusual in that it does not have to

---

[16] Texts about human nutrition, in particular, often refer to the 'omega-6 (n-6)' and 'omega-3 (n-3)' families of fatty acids. Omega-3 fatty acids are derived from alpha-linolenic acid and omega-6 fatty acids are derived from linoleic acid.

[17] Chapter 3 of McDonald *et al.* (2011) provides a detailed account of lipids (including fats) in the

diet, including the chemical structure of these substances.

[18] Scurvy is not a disease of humans only, but can occur in all animals that cannot synthesize vitamin C. For example, scurvy has been reported in captive capybara (Cueto *et al.* 2000).

be obtained from the diet, but can be manufactured in the body in the presence of sunlight. Zoo animals that are not exposed to sufficient natural light can become deficient in vitamin D, which, in turn, affects their calcium metabolism (see **section 12.8.2**).

Minerals

The greatest part of the animal body (about 96 per cent by weight) is made up of the elements oxygen (O), hydrogen (H), carbon (C), and nitrogen (N), because these are the major constituents of water and of most organic molecules. The remaining 4 per cent is made up primarily of calcium (Ca), phosphorus (P), potassium (K), sulphur (S), sodium (Na), chlorine (Cl), and magnesium (Mg), in that order (Schmidt-Nielsen 1997).

These elements are often referred to as 'macro-elements,'[19] or macronutrients, or macrominerals (or sometimes the major minerals). In addition, however, there are more than a dozen other elements that are found in the body, often as parts of enzymes, and which appear to be necessary for metabolic function, but only in tiny amounts. These are known as **trace elements**, or sometimes as 'microminerals' (McDowell 2003). None of these trace elements can be synthesized in the body by living organisms, so any metabolic needs must be met by dietary intake.

The major function of minerals in animals is in skeletal structures, such as bones, teeth, and shells, and eggshells in birds; other functions of minerals are as constituents of enzymes and hormones, and also as electrolytes, helping to maintain osmotic **homeostasis** within the body (McDowell 2003) (**Fig. 12.14**). The main minerals needed for normal life processes are listed in **Table 12.1**, although we should remember that there are still large gaps in our knowledge of what these elements are necessary for within the body, and what knowledge we do have comes largely from studies of laboratory, farm, and companion animals, not of wild animals.

Because health problems can be caused by both too much and too little of these elements (see

---

Figure 12.14 Calcium and phosphorus are important nutrients for bone and tooth development in vertebrates. These minerals are important for many invertebrate species too, particularly molluscs, such as snails, which need calcium phosphate to build their shells, as in the case of this African land snail *Achatina* sp. (Photograph: Grzegorz Polak/CC-BY-SA)

section 12.8.2), it is important to know, where possible, how much of these elements is present in diets fed to zoo animals. For example, insects such as crickets and fruit flies commonly fed to insectivorous birds, reptiles, and mammals appear to satisfy requirements for copper (Cu), iron (Fe), magnesium (Mg), phosphorus (P), and zinc (Zn) (based on our knowledge of domestic animal requirements), but some mealworms and waxworms are deficient in manganese (Mn) (Barker *et al.* 1998) (**Fig. 12.15**). A deficiency in either calcium or phosphorus can result in metabolic bone disorders, such as rickets or osteomalacia, in vertebrates.

Sometimes, knowing how much of a particular mineral is in an animal's diet still does not help us to predict whether the intake for that animal will be sufficient. Minerals can vary greatly in their **bioavailability**, which will depend on a variety of factors, such as the chemical form of the mineral or the presence of other minerals that may block absorption—and this leads us to consider interactions between minerals in the diet, because these substances rarely act in isolation within the body and the absorption of one mineral will be influenced by the presence (or absence) of another.

The relationship or ratio between different minerals is often as important, or more important, for

---

[19] Not all minerals are elements: some are frequently found as salts, which are compounds.

Mineral	Abbreviation	Some metabolic functions
MACROMINERALS		
Calcium	Ca	Major part of the mineral content of bone. Calcium metabolism in the body is very closely linked to phosphorus uptake and metabolism.
Chlorine	Cl	With sodium, makes up common salt (NaCl). Both sodium and chlorine are vital to the maintenance of osmotic homeostasis within the body. Chlorine also plays a key role in regulation of blood pH.
Magnesium	Mg	Diverse functions in body, from tooth and bone integrity to enzyme function.
Phosphorus	Ph	Major part of the mineral content of bone. Usually considered together with calcium.
Potassium	K	Osmotic balance (within cells). Transport of oxygen and carbon dioxide in the blood.
Sodium	Na	See chlorine. Vital in maintaining osmotic pressure within the body, particularly in extra-cellular fluids. Also transmission of nerve impulses.
Sulphur	S	Component of amino acids methionine, cystine, and cysteine. Also important component of bone, tendon, and cartilage structure.
MICROMINERALS		
Chromium	Cr	Important in insulin activity and glucose metabolism.
Cobalt	Co	Major constituent of vitamin B_{12}. Essential in the diet of ruminants for manufacturing vitamin B_{12}.
Copper	Cu	Growth, formation of blood cells. *Toxic in excess. Often considered together with molybdenum.
Fluorine	F	Tooth development. *Very toxic in excess.
Iodine	I	Constituent of thyroid hormones thyroxine and triiodothyronine.
Iron	Fe	Oxygen transport in the blood (iron is a vital component of haemoglobin) and other key biochemical reactions.
Manganese	Mn	Enzyme function; bone growth.
Molybdenum	Mo	Enzyme function. *Toxic in excess. Closely linked to copper metabolism (molybdenum and copper are antagonistic in the body).
Selenium	Se	Antioxidant function (closely linked to vitamin E). *Toxic in excess.
Zinc	Zn	Enzyme function. Zinc deficiency impacts on DNA, RNA, and protein synthesis in the body.

Table 12.1 Essential minerals

*All minerals can cause problems within the body both when they are deficient and when they are present in excess, although toxicity problems are better documented for some minerals (e.g. fluorine, molybdenum, and selenium) than for others.

Note: This list covers the main minerals needed for normal body processes, but is not exhaustive. Other trace elements, such as boron (B) and lithium (Li), are known to be required by some animal species. See McDowell (2003) for further information.

Figure 12.15 A gecko eating an insect. Feeding insects such as crickets appears to satisfy vertebrate dietary requirements for some minerals, such as magnesium, phosphorus, and zinc, but some mealworms and waxworms fed to vertebrates in zoos are deficient in manganese (Barker *et al.* 1998). (Photograph: David Gärtner/CC-BY-SA)

growth and health than the absolute amount in the diet (McDowell 2003). For example, the relationship between calcium and phosphorus in the body means that animals can be calcium deficient, even if there is enough calcium in their diet, if their diet also contains an excess of phosphorus. Ensuring that the diets of zoo animals provide the correct ratio of calcium (Ca) to phosphorus (P) is a major challenge for zoo nutritionists. The recommended Ca:P ratio in the diet for most mammals lies between 1:1 and 2:1 (the ratio in bone is slightly above 2:1); this dietary ratio should probably be higher in birds, but data are lacking except for poultry (Klasing 1998). Klasing (1998) also points out that smaller birds need proportionately more calcium for egg-laying than larger birds. This is for two reasons: firstly, small birds lay proportionately larger eggs; secondly, smaller eggs have proportionately more shell. Achieving the right Ca:P ratio in the diets of zoo animals is not always easy without calcium supplementation. For example, widely available grass hays, such as Timothy hays, have a very low calcium content in comparison with legume hays; cereal grains are also very low in calcium (McDowell 2003).

Other minerals that have documented antagonistic effects include copper (Cu) and molybdenum (Mo), with high levels of molybdenum in the diet limiting the retention of copper in the body. For example, a copper deficiency can give rise to a **wasting disease** in grazing ruminants, which is sometimes called 'salt sick' (McDowell 2003).

12.3 Guidelines and legislation on feeding zoo animals

In **Chapter 3**, we looked at the overall regulatory framework for zoos, and particularly for zoos in the UK. In this section, we provide a brief overview of the main legislation covering the provision of food and water for zoo animals, as well as non-legislative guidelines and other sources of information on zoo animal nutrition. However, it is worth noting that, in many countries, the legislation relating to the provision of food for zoo animals generally only covers the minimum requirements: that food and water should be made available, and that zoos cannot allow animals to starve. Good zoos will be concerned about providing optimum nutrition, which goes beyond simply the provision of enough food and water.

12.3.1 UK legislation on zoo animal feeding and nutrition

In the UK, as we saw in **Chapter 3**, the primary legislation regulating the activity of zoos is the Zoo Licensing Act (ZLA) 1981, as amended by the Zoo Licensing Act 1981 (Amendment) (England and Wales) Regulations 2002. The ZLA itself does not say very much about zoo animal nutrition, but, in England, zoo inspectors granting licences to zoos under the Act are required to take account of the Secretary of State's Standards of Modern Zoo Practice (SSSMZP) (Defra 2012a), which do make a number of detailed recommendations on feeding zoo animals.[20]

---

[20] Legislation in the UK does not prohibit visitors from feeding zoo animals, but the SSSMZP states that

'*Uncontrolled feeding of animals by visitors should not be permitted.*'

For example, section 2.1.1 of the SSSMZP states that:

> 'Food provided must be presented in an appropriate manner and must be of the nutritive value, quantity, quality and variety for the species, and its condition, size and physiological, reproductive and health status'.
>
> (Defra 2012a)

Other recommendations in section 2 of the SSSMZP deal with the health and hygiene aspects of the provision of food and water, including the requirement that '*Preparation of food, and, where appropriate, drink should be undertaken in a separate area suitably designed and constructed, and used for no other purpose*' (Defra 2012a).

The SSSMZP also state that '*Veterinary or other specialist advice in all aspects of nutrition must be obtained and followed*'. While vets do provide advice on nutrition at most zoos, at the time of writing only one zoo in the UK (Chester Zoo, in the north of England) has its own full-time in-house nutritionist. (Zoos in North America fare a little better, with in-house nutritionists at a number of leading zoos.)

Other UK legislation that impacts on how zoos feed their animals includes regulations resulting from the European Animal By-Products Regulation (EC) No. 1774/2002. In England, for example, the relevant national legislation is the Animal By-Products (ABP) Regulations 2005. **Chapter 3** provides further information and online sources for much of this legislation (largely from the Defra website).

Feeding of live prey

In the UK, it is illegal to feed live vertebrates and cephalopods (**Fig. 12.16**) to other animals, but acceptable to feed other live invertebrate species, such as locusts, crickets, and mealworms (Defra 2012a) (see **Box 12.2**). No other country has legislation restricting the feeding of live prey in zoos.

12.3.2 Legislation outside the UK on zoo animal feeding and nutrition

In the USA, the Animal Welfare Act (AWA) of 1966 requires, under the licensing arrangements

Figure 12.16 Aquarium exhibit or food item? In the UK, it is illegal to feed live vertebrates and cephalopods, such as this cuttlefish *Sepia latimanus*, to other animals, but in many parts of the world zoos do feed live vertebrate prey (such as fish). There are no restrictions in the UK on feeding live invertebrate species, such as crickets or mealworms, to zoo animals. (Photograph: Jeroen Stevens)

for zoos, minimum standards of provision of food and water. But the AWA applies only to certain species of mammals and not to all animal taxa (Vehrs 1996; Gesualdi 2001) (see **Chapter 3**).

In Australia, legislation varies between the different states and territories, but current animal welfare (animal protection) legislation generally includes the requirement that animals are treated humanely and are not neglected. Some territories have more specific legislation covering the provision of food and water. For example, the first part of section 8 of the Northern Territory of Australia Animal Welfare Act 1999 states that:

(1) A person in charge of an animal must provide the animal with food, drink and shelter—
   (a) that is appropriate and sufficient; and
   (b) that it is reasonably practicable for the person to provide.

12.3.3 Guidelines and other sources of information about zoo animal nutrition

In addition to meeting statutory requirements, zoos have access to a range of non-binding guidelines, and other sources of information on nutrition and food presentation. Feeding protocols are

Box 12.2 FEEDING LIVE PREY

The feeding of live vertebrate prey in zoos is not widespread. The provision of live fish is probably one of the few exceptions to this generally held rule: live fish are occasionally fed (for example, to species such as fishing cats) in some US, Australian, Asian, and mainland European zoos.

Studies have been undertaken that demonstrate that there are benefits to predatory species in being able to hunt live fish as prey (Shepherdson *et al.* 1993). In some rare examples, larger vertebrates are fed as live prey to zoo animals (live goats, chickens, and even cows are still routinely fed to large carnivores in at least one Chinese zoo).

Animals in the wild capture and eat live vertebrate prey, so why not in zoos? A survey of visitors to UK zoos suggested that there were few objections from the general public to the feeding of live invertebrate prey, even on-exhibit rather than off-exhibit, but more concern about feeding live vertebrate prey (Ings *et al.* 1997a). There also are various ethical arguments informing the decision, within the UK, to prohibit the feeding of live vertebrate prey to zoo animals; these are largely concerned with the welfare of both the potential prey and the potential predator. The first concern for the potential prey is that, in a zoo enclosure, it cannot escape the predator, as it might if the situation were played out in the wild. Although the prey may be able to hide or to elude the predator initially, all evasive behaviours within the confines of a zoo enclosure are likely only to prolong the

prey's potential state of stress before it is eventually caught and killed. There is good evidence that prolonged pursuits do severely compromise the welfare of prey species (Bateson and Bradshaw 1997). It is also easy to appreciate that well-fed captive-bred predators in the zoo may not be the efficient killers that their wild counterparts are, and therefore that any live prey species put into their exhibit may be at a greater risk of prolonged pursuit, and failed attempts at capture and killing, than would be the case in the wild.

There are also potential risks to the welfare of the predator when feeding live prey. It is possible that, in its attempts to survive, the prey may injure the predator by, for example, kicking or biting (e.g. Frye 1992). Given the great lengths to which zoos go to preserve the health and well-being of (valuable) animals in their collection, it seems rather perverse to threaten this routinely in order to deliver live food.

There are exceptions to this in relation to which there are clear benefits from feeding live prey and in which these benefits outweigh any potential costs. The obvious example is that of the potential predator being an animal due to be released into the wild as part of a **reintroduction** programme and the provision of live prey being a part of training before release. But even for animals that are part of a reintroduction programme, there are alternatives to the provision of live vertebrates as prey. One of these is carcass feeding, which is explored in more detail in **Box 12.6**.

---

available online to members of the Association of Zoos and Aquariums (AZA), via the nutrition sections of **Species Survival Plans (SSPs)**, and the AZA is moving towards open access on its website for much of this kind of information. The AZA also set up, or rather formalized, its own Nutrition Advisory Group (NAG) in 1994 (Dierenfeld 2005) (the full name of the group is the Nutrition Scientific Advisory Group, but it is still generally known as NAG).

The NAG has proposed a format for standardizing diet and nutrition information within **husbandry manuals** (for more details, see Fidgett

2005). It has also produced a series of technical papers on the nutrition of captive wild animals, which are available online at **http://www.nagonline.net**. For example, Fact Sheet 014 is entitled *Fruit Bats: Nutrition and Dietary Husbandry* (Dempsey 2004), and Fact Sheet 006 evaluates hay and pellet ratios for feeding zoo ungulates (Lintzenich and Ward 1997).

Another useful service provided by the NAG to AZA members is a current list of advisers on the nutrition of different species (again available via the NAG website), from tree kangaroos to the Komodo dragon *Varanus komodoensis*. These

advisers are drawn from the relevant TAGs and SSPs; some are zoo nutritionists, but most are senior keepers and curators with specialist knowledge of particular species or taxa.

A further useful source of information is the series of publications on nutrient requirements by the National Research Council (NRC) of the US National Academy of Sciences (**Box 12.3**).

Within Europe, the equivalent zoo organization to the AZA in North America is the European Association of Zoo and Aquaria (EAZA). Zoos can obtain information on nutrition for their animals from what is now called the EAZA Nutrition Group (ENG)[21], which started life as the European Zoo Nutrition Research Group (EZNRG) at a meeting in Rotterdam in 1999. EAZA does not produce or

distribute diet sheets for particular species, but, like AZA, does provide information on nutrition within husbandry manuals. So an EAZA member zoo wanting to find out how to feed a species new to their collection would be likely, as a first step, to consult the most recent **taxon advisory group (TAG)** manual. There is also much useful information about zoo animal nutrition available online via the EAZA website at **http://www.eaza.net**.

Zoos can sometimes be wary of sharing or disseminating diet sheets for their animals. Local conditions may dictate that different diets are needed in different areas (for example, some areas may have a mineral deficiency in their grazing, such as a lack of selenium). It is also risky to assume that a generic diet will be suitable for

[21] The EAZA Nutrition Group should not be confused with the European Zoo Nutrition Centre (EZNC). The latter is an independent group, and its recommendations are not endorsed by EAZA.

Figure 12.17 A generic diet is not necessarily suitable for all members of a taxonomic group. Among monkeys, for example, there are differences in vitamin D metabolism between Old and New World species. In New World primates, such as this golden-headed lion tamarin *Leontopithecus chrysomelas* (shown here eating a mealworm), vitamin D_3 is many times more potent than vitamin D_2, whereas Old World primates are able to utilize both forms effectively. (Photograph: Jeroen Stevens)

all members of a **taxonomic** group (**Fig. 12.17**). Among monkeys, for example, vitamin D metabolism is different for Old World and New World monkeys. Vitamin D comes in two forms: D_2 (ergocalciferol) and D_3 (cholecalciferol). In New World primates, vitamin D_3 is many times more potent than vitamin D_2 (Hunt *et al.* 1967). So zoos need to know which type of vitamin D has been added to a commercial primate diet.

12.4 Working out an animal's dietary requirements

We have already said (**section 12.2.2**) that the nutritional requirements of an individual animal will depend on its physiology, behaviour, metabolism, and anatomy. These requirements are not static within an animal's life cycle, but will change with age, level of activity, health, and reproductive status.

For example, birds that moult will need additional nutrients at that time, and female birds will need extra nutrients prior to egg-laying. Within the same species, different sexes may have different nutritional requirements. Female mammals will require additional food during gestation and, in particular, during lactation, when energy requirements may rise sharply in many species. (For a review of energy requirements during reproduction in mammals, see Gittleman and Thompson (1988).)

The diets[22] fed to zoo animals must meet both the general energy or metabolic requirements of the animal and also its specific nutrient requirements. In other words, zoos have to work out both how much food to provide in total and what the nutrient composition of that food is, or should be, so that nutritional requirements are met. In practice, it is often easier to start with the basic nutritional requirements of an animal (for example, 10 per cent protein) and then work out food quantities that meet these requirements. Of course, this is not always as straightforward as it sounds; formulating diets for wild animals in captivity is a complicated business and there are many factors that need to be taken into account.

Crissey (2005) has provided a useful nutrition matrix that can be adapted to different species and different circumstances. This takes into account not only factors such as nutritional requirements and food quantities, but also the health status of the animal and any management constraints. But even with tools such as Crissey's matrix, a recurring problem is that zoos often do not have adequate information about what the basic nutrient requirements of wild animals are, particularly with regard to trace elements. We will return to this problem in **section 12.4.4**.

It is also worth noting here that zoo animal nutrition has only relatively recently become the focus of specific scientific investigation. It was not until 1994, for example, that the American Association of Zoos and Aquariums (now the AZA) first recognized nutrition as a 'scientific advisory

---

[22] Diet is not the same thing as nutrition. The word 'diet' can mean slightly different things in different contexts, such as the usual food given to an animal, or a restricted selection of foods given for medical reasons.

Box 12.4 THE HISTORY OF ZOO ANIMAL NUTRITION

The importance of minerals such as calcium and phosphorus in animal diets was not widely recognized, or was not considered important, until the early twentieth century (Ammerman and Goodrich 1983). Vitamins were not 'discovered' until the twentieth century and, even today, there are still considerable gaps in our knowledge of essential nutrients for many animal species.

The incidence of diseases such as rickets in captive animals prompted some early experimental analysis of the role of nutrition in maintaining zoo animal health. For example, in the 1930s cebid monkeys at Philadelphia Zoo were allowed to range freely and to self-select dietary items.

The resulting dietary recommendations published by Dr Ellen Corson-White, of the University of Pennsylvania, were based on a combination of what the animals chose to eat and known nutritional requirements (Corson-White 1932; Dierenfeld 1997a).

In the 1960s, Dr Hans Wackernagel of Basel Zoo in Switzerland developed a range of formulated pelleted diets for various taxa of exotic species and also provided details of the nutrient composition of these manufactured diets. But it was not until the 1970s and 1980s that zoos in the USA, and then in Europe, first started to employ in-house professional nutritionists.

speciality' (Dierenfeld 1997a); **Box 12.4** provides a brief overview of the history of zoo animal nutrition. This is perhaps surprising, given the long history of zoos. But as Oftedal and Allen (1996) point out, in the past many zoo animals managed to survive for considerable periods of time on what we would now regard as inappropriate diets and, because the animals were not dying, or at least were not dying in huge numbers, there was little pressure on zoos to investigate whether or not diets could be improved.

Even in good zoos today, the diets provided for the animals can be driven more by tradition than science, and the *Zoos Expert Committee Handbook* (Defra 2012b) warns that diets can suffer from **dietary drift** and can be changed incrementally over time by keepers (not always for the better). The *Handbook* counsels that diets should be subject to regular review, and also recommends that zoos should make use of the services of a nutritionist to support keepers and veterinary staff in delivering appropriate diets for the animals in their care.

12.4.1 Working out how much food to feed

To calculate the general energy requirement of an individual animal, one of the first things that a zoo

needs to know is the animal's weight (we shall see why shortly). Working out the weight of a zoo animal is not as easy as it sounds, particularly for an elephant or a giraffe, although some animals can be trained to step onto scales (**Fig. 12.18**). Many zoos build weigh bars into low platforms within an enclosure, often across a doorway, so that the animal becomes accustomed to stepping onto the platform.

In addition to knowing an animal's weight, the zoo needs to know how much energy the animal

Figure 12.18 At Singapore Zoo, a giant tortoise *Geochelone gigantea* is being trained to step onto scales for weighing. Knowing the weight of an animal is a vital first step in calculating its general energy requirement and hence how much food to provide. (Photograph: Diana Marlena, Singapore Zoo)

needs to sustain its basic metabolism. A term often used in relation to an animal's energy requirement is **metabolizable energy (ME)**. Confusingly, ME refers to the energy content of the food (along with gross energy and digestible energy), not to the energy requirement of the animal.

Terms used in relation to energy requirements are:

- gross energy (GE), which is the total energy in the food;
- digestible energy (DE), which is GE minus the energy lost in faeces;
- metabolizable energy (ME), which is DE minus energy in urine and gaseous products of digestion.

Therefore, ME is the energy available to satisfy the animal's metabolic requirements. This is the energy that the animal needs to sustain its basic metabolism or basal metabolic rate (BMR), plus energy for activity, plus energy needed for growth, thermoregulation, and any other processes, such as egg-laying in birds or reptiles (e.g. Klasing 1998).

The basal metabolic rate has been measured for many mammal and bird species (e.g. Robbins 1993) and, for any given taxonomic group, this value is closely correlated with body weight. Birds have a higher metabolic rate than mammals of equivalent size, whereas reptiles have a lower metabolic rate than mammals of the same size.

Once the zoo knows the weight of an animal, there are published equations for mass-specific BMR (see Robbins 1993) which can be used to calculate the minimum energy requirement per day for that animal (although it is worth noting that there is still considerable debate about the detail and usefulness of some of these equations). Of course, the BMR is only the starting point and the animal will need additional energy for activities such as running or flying. These sorts of activity can 'cost' between five and ten times BMR.

The software package **Zootrition**™ (see **section 12.4.3**) has an energy requirement module that will calculate BMR on the basis of several different equations. The user can then pick the one that he/she feels is most appropriate for the species. Zootrition™ will also calculate the field metabolic rate (FMR), or the energy that an animal needs to survive and be active, based on various levels of activity and life stages. In practice, however, it is fairly unusual for a zoo to be confronted with an animal new to its collection that does not arrive with an accompanying diet sheet, or at least some basic dietary information.

How much food is actually given also depends on an assessment of activity and on factors such as whether the animal is solitary, or housed within a social group, in which case other animals may eat some of its food. For taxa such as **herps** and fish, zoos often feed reactively—that is, they feed slightly more than the calculated amount and then adjust feeds on a daily basis depending on how much is left uneaten. The energy requirements of homeothermic animals also depend on external temperature; these animals need more food when it is cold just to maintain body temperature. In practice, energy requirement estimation is just that—estimation. It is vital to monitor body weight (ideally directly, but, if this is not possible, then through alternatives such as **body condition scoring** (see **Box 11.1**) and to adjust the diet quantity if animals become underweight or overweight.

As we have seen already in this chapter, however, not all the content of food provided for an animal will be available to meet its energy requirements. Any foodstuff will comprise digestible matter, indigestible matter, and also material that can be broken down by fermentation in the gut. The relative proportions of these three components will determine the overall availability of energy from the diet.

The digestible matter comprises the carbohydrates, fats, and proteins that we discussed in **section 12.2**. Fermentable materials are not broken down by the animal itself, but by the symbiotic gut microflora, particularly in ruminants. Finally, some compounds (for example, lignin) are not broken down at all in the gut and cannot be used as a source of energy; this matter simply passes through the gut and is excreted in the faeces.

Component or fraction of foodstuff	Nutritional terminology explained
Crude protein	Essentially, the protein content of a food is determined by analysing the nitrogen (N) content, because all proteins contain approximately 16 per cent nitrogen. But there will be some nitrogen in foods that is not from proteins, so the value obtained from an analysis of the nitrogen content of a foodstuff is referred to as the crude protein fraction, rather than the true protein fraction.
Ash	This is the inorganic content of a foodstuff (e.g. calcium, phosphorus, copper, iron, and other minerals). It is determined by heating (burning) a weighed sample of the foodstuff at a very high temperature, to remove all of the carbon. The ash is the residue left over after this process.
Fat	The fat content of a foodstuff can be given as crude fat, which is all the material that will dissolve in a solvent such as ether, or total lipids, which involves a different extraction method using acid hydrolysis and gives the lipid content, excluding substances such as resins or waxy materials.
Neutral detergent fibre (NDF)	This is the entire non-soluble fibre content of the foodstuff (and includes cellulose, hemicellulose, and lignin). The term 'detergent' refers to the chemicals used to separate out the non-soluble fibre from other components of the foodstuff. Total dietary fibre is the entire fibre content (soluble and insoluble) of the foodstuff and is a more useful term for animals with minimum gut fermentation.
Acid detergent fibre (ADF)	This is the NDF minus the hemicellulose. It is partially digestible to varying degrees, depending on species. Here, acid, as well as detergent is used to separate out the indigestible fibrous material.

Table 12.2 Nutritional assay terminology

Note: For further information on nutritional analysis and on animal nutrition in general, we recommend *Animal Nutrition* (McDonald *et al.* 2011), now in its seventh edition.

But how can zookeepers find out how much digestible material there is in a particular food item? And how can nutrient intake be measured accurately if an animal does not eat all the food that is provided? Oftedal and Allen (1996) summarize this problem nicely when they talk about distinguishing between '*the diet as presented*' and '*the diet as consumed*'.

12.4.2 How can the nutrient content of the diet be measured?

Questions about the amount of digestible material in an animal's diet can be answered by carrying out food intake studies, within which the total amount of food provided is carefully weighed, and then uneaten food and faeces are also weighed and analysed. The BIAZA *Zoo*

Research Guidelines on Nutrition and Diet Evaluation (Fidgett and Plowman 2009) provide information on this kind of analysis.

Establishing the nutrient content of a food item, such as a grass hay or another type of forage, is done by laboratory analysis. A typical analysis produces data on the crude protein, ash, fat, and fibre content in the food, expressed as proportions of the total **dry matter**[23] (that is, the weight of the food without water). **Table 12.2** provides a brief explanation of some of the terminology used in a basic laboratory analysis of the nutrient content of a foodstuff.

Thus, different types of study (food intake studies and laboratory analysis of the nutrients

[23] Nutrient values are usually reported on a **dry matter** basis to remove any variability between feeds due to differing moisture content.

Figure 12.19 It is particularly difficult to analyse the nutrient content of a diet when an animal is fed a mixture of different food items, such as the nut, dried fruit, and seed mix provided for this steppe lemming *Lagurus lagurus*. This mixture of foodstuffs may be nutritionally balanced, but the animal may feed selectively on just some of the items offered. (Photograph: Kathi Herrmann)

12.4.3 Zootrition™ and other dietary analysis software for use in zoos

Zootrition™ is a nutritional software package and database originally developed by Dr Ellen Dierenfeld, a leading zoo animal nutritionist now based at Saint Louis Zoo, Missouri (Dr Dierenfeld was previously at the Wildlife Conservation Society (WCS) and Bronx Zoo).

The Zootrition™ software package was developed specifically for use by zoos to help to ensure that the nutritional composition of the diet that they give to their animals is correct. Zootrition™ does this by providing a database of nutrient composition values for more than 2,500 feeds, including whole prey items such as mealworms, crickets, and mice. This database allows the nutritional content of specific food items to be compared and also allows the overall nutritional make-up of an existing or proposed diet to be calculated. Further information about Zootrition™ can be found on the Zootrition website, at **http://www.zootrition.org**.

At the time of writing (November 2012), the EAZA Nutrition Group is planning a new dietary analysis platform. This will be called 'Fauna' and is planned for release in 2013; further information can be found on the EAZA website.

12.4.4 Working out what nutrients an animal needs

Even with databases such as Zootrition™ available to zoos, there is still a paucity of information about the precise dietary requirements of wild animals. As we have seen earlier in this chapter, nutrient requirements have been determined in considerable detail for domesticated animals, such as the cow, sheep, horse, pig, cat, dog, and chicken, and also for a very small number of wild animal species, for example the white-tailed deer *Odocoileus virginianus* (e.g. Thompson *et al.*1973) (**Fig. 12.20**). But how similar, for example, is a tapir to a horse in its nutritional requirements?

The problem of a lack of data on baseline nutrient requirements for zoo animals is more acute for birds than for mammals. Nearly all data on

in particular food items) can help zoos to decide how much food to provide and whether the diet is providing all the necessary nutrients. But both these sorts of study can be laborious and time-intensive to carry out. A food intake study for a bird or mammal fed on a proprietary seed mix, for example, would involve separating out each type of nut or seed in the mix before weighing each of these, and then the even more laborious job of picking up the uneaten seeds from the enclosure afterwards, and sorting and weighing the leftovers (**Fig. 12.19**). Nutrient assays in the laboratory are also relatively expensive and a zoo that wanted to sample all its forages on a regular basis, or wanted a detailed analysis of vitamin and mineral content of its foodstuffs, would very quickly run up a large bill for laboratory assays.

Fortunately, zoos now have access to computerized databases that can provide much of this sort of information. The best known of these databases is Zootrition™.

Figure 12.20 The white-tailed deer *Odocoileus virginianus* is one of very few species of wild animal for which detailed nutrient requirements have been determined. In general, zoos must use nutritional models developed for domesticated animals, such as the cow, sheep, goat, and horse. (Photograph: Scott Bauer)

avian nutrient requirements come from studies of granivorous domestic species (particularly the chicken). Domestic poultry species do not provide an adequate nutritional model for non-granivorous birds such as carnivorous storks or birds of prey,[24] or for birds that are fruit eaters, or nectar feeders, or true herbivores (Klasing 1998).

There are fewer data still for non-mammalian and non-avian vertebrates. There are some data on nutrient requirements available for fish, from the **aquaculture** industry, but virtually no data on baseline nutrient requirements are available for most reptiles and amphibians.

Studies of the diet of wild animals do exist, albeit for a very limited range of species, and these can provide valuable pointers to zoos for the development of appropriate diets for their animals. The findings of some of these studies should be treated with caution, however, because they may be based on data from only one season; this is not particularly helpful when there is strong seasonal variation in food supply.

Another problem is that the nutrient content of wild versus domestic varieties of fruits and

vegetables is not standard. For example, an animal that is known to eat figs in the wild may be given figs in captivity. But a study by Silver *et al.* (2000) of the foods consumed by black howler monkeys *Alouatta pigra* in Belize showed that the calcium content of wild figs may be seven times greater than that of figs from a domesticated cultivar. Similar findings were reported in a study of bat feeding preferences in Panama (Wendeln *et al.* 2000).

12.5 The supply of food

Having looked at the theoretical background to feeding zoo animals, what about the practicalities? Where do zoos obtain food for their animals, and what are the main considerations that zoo managers and keepers must take into account when sourcing food items?

12.5.1 Where does the food come from?

In addition to grasses and hays, three main categories of foodstuffs are consumed by zoo animals, generally cited as follows:

- produce[25]—food such as fruit, vegetables, meat, fish, dairy produce, and tinned or frozen foodstuffs;
- commercial formulations—foodstuffs such as pelleted food or concentrates, as well as formulated diets (for example, seed mixes for birds);
- browse—plant material other than grass or hays (for example, willow branches and leaves).

Produce

Produce is generally supplied by companies that also supply the human food industry, so this is usually food that is considered 'fit for human consumption' and, as such, it is subject to the same

---

[24] For birds of prey or other avian carnivores, the domestic cat—as another carnivore—may provide a more appropriate nutritional model than the granivorous chicken.

[25] Produce and other terms used to describe foodstuffs vary among countries. Zootrition™ uses US terms that may not always be familiar to zookeepers in Europe and the rest of the world.

strict health and safety regulations as the food that we buy in supermarkets.

Ideally, the dietary requirements of the animals in a collection will be calculated and appropriate produce purchased accordingly from wholesalers. However, some zoos also incorporate, to a greater or lesser extent, surplus produce items into their animals' diets. Surplus produce is those items that are given away freely by wholesalers or supermarkets at the end of the working day or week. This can offer considerable cost savings to zoos and allow limited zoo finances to go further, but caution should be exercised when using surplus food. Although such produce is fit for human consumption, the type of surplus food items that are available may not be ideal for the animals and may not contribute very much to meeting their optimal nutrient requirements. For example, many supermarkets have surplus bakery goods that are readily available, but bread and buns are generally not ideal foodstuffs for most zoo animals.

Commercial formulations

Foodstuffs are also purchased by zoos from dedicated commercial animal food suppliers, for example those supplying livestock farmers and the pet industry. There are also some specialist zoo foodstuff supply companies, such as Mazuri Zoo Foods® and Nutrazu®. Foodstuffs from these sources are either specific food items, or specially processed or formulated foodstuffs.

Specialist food items purchased by zoos include live food (for example, invertebrate prey items such as crickets or mealworms) and other foodstuffs, such as nectar. Formulated foodstuffs are mixes of ingredients (for example, seed mix) or a combination of ingredients that are processed into pellet form; the latter are usually referred to as concentrates, but can variously be called nuts, biscuits, dry diets, or chow (for example, monkey chow). Because all the ingredients that go into these formulations are known, it makes it easier to assess the nutritional composition of the diet.

In other words, if an animal is fed solely on a commercial formulation, the zoo will have easy access to information about the nutritional intake (protein, vitamins, minerals, etc.) of that animal.

Another benefit to zoos of using food concentrates is that non-nutritional ingredients can be added to formulations. For example, pelleted food may contain additional roughage, to improve the digestibility of the diet, or an **anthelmintic drug**.[26] The addition of such drugs to formulated diets allows zoos to treat their animals for parasitic worms without having to capture the animals to dose them.

Browse

Zoo grounds can be a great source for animal feed. Zoo enclosure design should, ideally, ensure that grazers and browsers have sufficient vegetation within their enclosure to meet their needs, but browse can be supplemented by plant material from elsewhere within the zoo grounds, or with material that is brought in from outside the zoo (for example, from a local park that needs to prune its trees). Finding sufficient browse is a greater challenge for smaller city centre zoos than it is for larger wildlife parks. The provision of browse is also a challenge for some specialist feeders that require vegetation that cannot be sourced locally, such as bamboo and eucalyptus leaves for giant pandas *Ailuropoda melanoleuca* and koala bears *Phascolarctos cinereus*, respectively (**Fig. 12.21**). Care must be taken to feed the right browse, and to avoid plant species which are toxic (see **Box 12.1**).

However, concerns about possible toxicity of browse should not prevent zoos from trying wherever possible to feed browse to animals such as giraffes. Where fresh leaves and branches are limited in availability, browsing animals are often fed hays instead (grass hay or alfalfa hay are commonly used), and this can sometimes lead to nutritional deficiencies and health problems (e.g. Koutsos *et al.* 2011).

---

[26] An **anthelmintic** (or **antihelmintic**) **drug** is a drug that is used to treat parasitic worms, such as roundworms or tapeworms. The word **helminth** is often used to refer to parasitic worms found in the gut.

Figure 12.21 Giant pandas *Ailuropoda melanoleuca* are specialist feeders, adapted to a diet consisting mainly of bamboo. Most zoos cannot obtain sufficient bamboo all year round to feed giant pandas, so must substitute nutritionally equivalent plant material. (Photograph: © Klass Lingbeek-van Kranen, **http://www.iStockphoto.com**)

Even when zoos do have access to ready sources of browse, information on the appropriate amount of browse to feed is hard to come by. For example, keeper's notes may record that two or three branches of browse are supplied to each animal each day. But this does not describe how much edible material per branch is available to the animal. Large branches cannot easily be weighed, and neither weight nor volume gives much information about the amount of edible material (leaves, smaller twigs, and bark) available to the animal. In a detailed study of the feeding behaviour of moose *Alces alces*, Clauss *et al.* (2003) found that branch diameter at the point of cutting was closely correlated with the amount of foliage and edible twigs on the branch. This correlation held true for nine different tree species, including commonly fed browse species such as willow, hazel, and oak.

12.5.2 Other considerations

As well as finding appropriate supply sources for foodstuffs, zoos must take into account other considerations when sourcing food for their animals, such as the nutritional composition of the food, **biosecurity**, seasonal variation in supply, and ethical issues relating to feeding zoo animals.

Variation in the nutritional composition of food

It is highly likely that the nutritional composition of produce from a supplier local to a zoo will be different to that of the same produce found in the animal's natural habitat. The nutritional composition of plant foods will also vary according to species or variety (**Fig. 12.22**), the climate and/or season when it was grown, the soil in which it was grown, and the size and age of the fruits, leaves, or shoots. Plant material also varies in nutritional composition from one part of the same plant to another; for example, younger grass shoots are more nutritious than older stems.

Luckily, the study of **agronomy**, and the economic importance of farm animals such as cattle and sheep, means that we know a lot about the physiology of grazing livestock, and also about the impact of different types of cereals and forage on the development, growth, and reproduction of these animals. Data from studies of domesticated grazing animals inform us that, although grass and grass-related crops may all look broadly similar, there is considerable variation in nutritional content between raw grass and forages, such as hay[27] and straw. Other forms of stored forage include silage, which is fermented fodder, and haylage, which is a semi-fermented forage with a moisture content that is higher than that of hay, but lower than that of silage.

Supplements

It is one thing to work out what an animal's nutrient requirements are and quite another to be sure that all these nutrients are provided in the correct quantity in the animal's diet. Sometimes, even if the nutritional value of foodstuffs has been carefully calculated, zoos will still need to add supplements such as vitamins and minerals to the produce fed to their animals. For example, calcium powder is often sprinkled onto fresh produce fed to reptiles, to reduce the risk of the

---

[27] **Hay** is produced by drying grass; **straw** is the dried stems of cereal crops, such as wheat or barley.
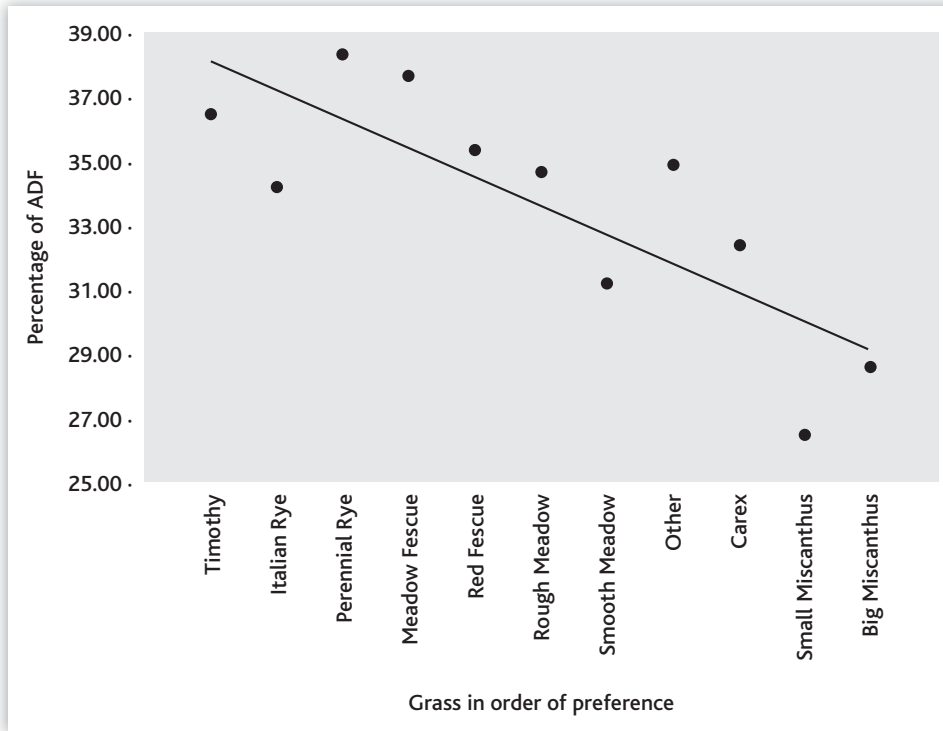
Figure 12.22 This scatter plot shows a significant correlation between the acid detergent fibre (ADF) content of different grass and other plant species, and the grazing preferences of captive zebras in zoos in UK and Irish zoos. The zebras in this study preferred grass species with a low ADF. (Reproduced with permission from Armstrong and Marples (2005))

development of metabolic bone disorders (see **section 12.8.1** on nutritional diseases).

Often, commercial formulations are available that already contain added quantities of vitamins and minerals. This helps to avoid the problems inherent in administering supplements in tablet form, for example. Supplements can also be added to invertebrate prey items such as crickets; a number of suppliers of foodstuffs for **exotic animals** offer 'gut-loaded' crickets or locusts containing additional calcium, although there is little hard evidence for the effectiveness of this.

Biosecurity and animal health

Part of the process involved in sourcing food is ensuring that the food is safe for zoo animals to eat. For many of the foodstuffs purchased by zoos, this is redundant, because the produce is considered 'fit for human consumption' and, as such, is governed by rigorous standards of hygiene. But

for zoo foodstuffs that do not come under the banner of 'fit for human consumption', zoos must ensure that their biosecurity is not compromised when bringing produce into the zoo.

The need for zoos to maintain a high level of biosecurity at all stages of food sourcing and preparation cannot be overstated. For many foodstuffs, this means ensuring that zoos make their purchases from reliable wholesalers, whose methods of storage and transport meet high standards so that foods do not deteriorate or become contaminated before they reach the zoo. Even if zoos are careful to use reliable suppliers, there are still additional steps that can be taken at the zoo to reduce the adverse consequences of any lapses in biosecurity. For example, freezing food items can reduce the likelihood of parasite transfer from meat and associated by-products to zoo animals, because many endo- and exoparasites cannot survive the freezing process (e.g. Deardorff and Throm 1988). Keepers and

other staff involved in food preparation also need to check foodstuffs for non-biological contaminants, such as stray pieces of wire or baler twine in hay.

Transport costs and environmental impact

The term 'food miles' is often used nowadays as an indicator of how much energy is required to transport a foodstuff from its source to its place of consumption. For example, for a UK zoo, the food miles for apples or pears from a local orchard would be very low in comparison with the food miles for pineapples flown in from Africa, but the nutritional composition of these fruits may not be substantially different.

If zoos wish to be seen as sustainable and environmentally responsible organizations, they need to take into consideration the costs of transporting their foodstuffs. Importing bamboo or eucalyptus leaves, or even pineapples or bananas, can clock up a high total of food miles and have an adverse effect on the zoo's environmental impact and carbon footprint (see **Chapter 15**).

Seasonal variation in food supply

Obtaining sufficient browse for zoo animals outside the summer months is a particular challenge in temperate climates, where deciduous trees shed their leaves in winter. Some zoos are now experimenting with freezing browse, although, given the large volume of freezer space required, this is an energy-intensive option (and may also affect palatability). Another alternative is the production of browse silage for use in the winter months. This offers an inexpensive alternative to freezing browse and has been used at Zurich Zoo for some years (Hatt and Clauss 2001).

Ethical considerations in sourcing animals as foodstuffs

When sourcing animals as food items for other animals, zoos have a duty of care to ensure that the production (life) and death of the food animals is such that it does not compromise their welfare (Spencer and Spencer 2006) (see **Box 12.2** on feeding live prey). It is still common practice in some zoos to breed and rear larger ungulates (for

example, deer) partly for exhibit, but also to use 'surplus' animals as food for carnivores within the collection. Again, the zoo is directly responsible for the welfare and humane culling of these animals.

Although the legislative framework within the UK prohibits the feeding of live vertebrate prey, zoos can, and do, feed live invertebrate prey items. The most common invertebrate species fed in zoos are crickets, locusts, mealworms, and daphnia. Many of these species will be bought live by zoos (from specialist breeders) and fed soon after, but some zoos will choose to rear these animals themselves. Zoos still have a duty of care for these animals, to ensure that their welfare is not unduly compromised during their lifetime.

Our knowledge of how invertebrates perceive physiological or psychological **stimuli** is still relatively poor, although there has been a welcome recent increase in research in this area (e.g. Elwood 2011; Mason 2011). We do know that invertebrates will avoid certain toxic and noxious stimuli, such as extremes in temperature and light (Sherwin 2001). Therefore it follows that, while these animals are stored prior to being fed, they are provided with the appropriate conditions necessary to ensure that the **five freedoms** are satisfied (see **Chapter 7**). As such, they should be given adequate food, water, and shelter in an area that is kept at a suitable temperature and humidity.

12.6 Food storage and preparation

Foodstuffs purchased by a zoo are rarely used straight away, but will need to be stored for varying periods of time. This may be for only a few hours for some fresh produce, or up to several months for dried or frozen foods. While food is in storage, the zoo has to ensure that it remains fresh and palatable, safe to eat, and does not lose a significant proportion of its nutritional value.

12.6.1 Avoiding contamination of food

Measures to prevent the contamination of food during storage and preparation, and to reduce

Figure 12.23 Keepers at Paignton Zoo Environmental Park preparing a variety of fresh foodstuffs for the zoo animals. (Photograph: Paignton Zoo Environmental Park)

the risk that foodstuffs may be vectors for disease, should be an integrated part of good husbandry (**Fig. 12.23**). This includes everything from the keepers' personal hygiene (washing hands, not wearing 'work' clothes outside the zoo, etc.) to cleaning food preparation areas and equipment thoroughly and regularly.

All this may sound rather obvious, but these sorts of measures are essential components of good biosecurity, and are just as important for the health of keepers and other zoo employees as they are for the health of zoo animals.

Zoos also need to take measures to exclude **pests** such as rats, mice, and cockroaches from food storage and preparation areas. Pest control in relation to food preparation and storage can be achieved through a variety of steps, all of which reduce the impact of pest species on other captive animals. It should be remembered that many pest species are opportunists and thus will take

advantage of resources that are easy to access. Therefore zoos need to make access to food, and to other resources that pests may find attractive, as difficult as possible—in other words, to have good biosecurity. This can be as easy as ensuring that tightly fitting lids are replaced on food containers, doors to food storage and food preparation areas are kept shut, and food is not left in 'non-secured' areas (for example, if food is prepared in advance of feeding, it should not be left in open buckets from which pest species may be able to access it) (**Fig 12.24**).

12.6.2 Maintaining palatability and nutritional value

The palatability and nutritional value of food can be greatly affected by the conditions in which it is stored. Fortunately, food science and technology is a well-established discipline that has taught us a great deal about good food hygiene and the processes underpinning decay in foodstuffs. (There is a huge literature on food storage and food decay; although this is largely about food intended for human consumption, much if not most of this information is also relevant to the preparation and storage of food for animals.)

The process of decay in foodstuffs is complex, and varies considerably depending on the type of food and the conditions in which it is stored. Heldman (2003) provides much useful information about food processing and storage, and about the deterioration of foodstuffs over time. In general, however, harmful micro-organisms in foodstuffs will proliferate much more rapidly in warm damp conditions, so optimal food storage conditions will usually be found somewhere that is both cool and dry. Fresh foods are most susceptible to deterioration, and the process of denaturing or decay is exacerbated by extremes of light, heat, and moisture, and by exposure to micro-organisms such as bacteria and moulds. Storing fresh foodstuffs in a refrigerator at temperatures of around 1–4°C (34–40°F) is generally regarded as optimal. Below this temperature range, fresh fruits and vegetables will freeze, and their texture

Figure 12.24 Grey-crowned cranes *Balearica regulorum* at Warsaw Zoo, with feral pigeons attempting to gain access to the food provided for the cranes. This sort of access by avian pest species is difficult to prevent completely, even within aviaries, but pest species such as pigeons, or rats and mice, can transmit diseases to zoo animals. (Photograph: Barbara Zaleweska, Warsaw Zoo)

and palatability will change; above this temperature range, micro-organisms, such as bacteria, will proliferate much more rapidly.

Zoos also make extensive use of freezers for food storage, particularly of meat and fish. Here, foodstuffs are generally stored at temperatures below −18°C (0°F); lower temperatures of −28°C (−19°F) are recommended for fish by some sources to reduce deterioration and loss of nutrients (e.g. Heldman 2003). Care should be taken that frozen foods are thawed thoroughly before being provisioned, and that foodstuffs are not frozen, thawed, and then refrozen. Frozen fish should be thawed overnight in a refrigerator, rather than by immersion in cold or running water, to avoid the loss (leaching) of water-soluble nutrients (Whitaker 1999).

There is a particular risk to animal health associated with the use of frozen fish because of the action of enzymes (thiaminases) produced during thawing. However carefully fish is thawed, there will be some degradation and loss of thiamine (vitamin B$_1$). This means that thiamine needs replacing in the diet of fish-eating animals and, along with vitamin E (which is also lost during storage), thiamine is routinely given as a supplement to piscivores fed on a diet containing frozen fish to reduce the risk of the development of neurological disorders (Geraci 1986).

To reduce the risk of deterioration in food quality, zoos need to minimize any lag time between the preparation of food and its consumption. Both storage and preparation can alter the nutritional content of foodstuffs, which means that the animals may not be consuming the nutrients that we hope they are. Compared with other nutrients, vitamins are not particularly stable and can lose their activity over time, particularly if exposed to high temperatures. Vitamin C, for example, can

be lost more or less completely from foodstuffs stored for six months or more (Klasing 1998). On the plus side, however, most vitamins are not expensive to manufacture, so supplementation is not particularly costly.

12.7 Food presentation

After appropriate food has been sourced and stored, it needs to be provided to the animals in the zoo. It may seem an obvious point to make, but if foods are provided to zoo animals with the intention that they should eat them, then the food needs to be accessible (**Box 12.5**).

12.7.1 Access and availability

There are numerous differences between individual animals of the same species (for example, age, social rank, health status, and intelligence), and these factors will affect the ability of different animals to gain food. Not all animals may be able to gain food from all areas of the enclosure, or from complicated feeding devices. Therefore the method used to provide food needs to make allowances for these individual differences within a group of animals to ensure that each animal in a socially housed group can gain access to a nutritionally complete diet. For example, many **mixed-species exhibits** will hold animals that have different dietary requirements and yet share an enclosure. By considering favoured areas or areas to which some species can gain access and others cannot, different diets can be provided within the same environment.

One of the most widely used methods of feeding wild animals in captivity is often referred to as **cafeteria-style feeding (CSF)** (Marqués *et al.* 2001). This is where a variety of foodstuffs are

---

Box 12.5 **WHY DO KEEPERS CHOP UP FOOD FOR ZOO ANIMALS?**

Many keepers will lament that they spend much of their day chopping up food for animal feeds. But why is it necessary to chop food for animals in zoos? After all, wild animals do not have this assistance in accessing and processing their food.

For some species, it may be necessary to chop food so that it can be mixed up, to try to prevent the animals choosing between foodstuffs offered and so ensure that they consume a nutritionally balanced diet (see **section 12.7.2**). Similarly, if food supplied to socially housed animals is not chopped up, keepers may be concerned that dominant animals will get priority access to favoured foods and that the subordinates will not get a nutritionally balanced diet. In fact, a study by Plowman *et al.* (2008) demonstrated that when groups of Sulawesi crested black macaques *Macaca nigra* and red-ruffed lemurs *Varecia rubra* were fed two different diets, one composed of chopped foods and the other of the same foodstuffs presented whole, the overall food intake of the individual animals did not differ.

For many species in zoos, it seems that food is chopped or peeled out of habit. We have suggested already in this book that much housing and husbandry practice in zoos is not influenced so much by research, but more by tradition. Sometimes, this can be invaluable, but sometimes it can be nonsense. Providing whole foods to zoo animals has been demonstrated to be enriching, because the animals are stimulated cognitively and physically in order to handle and access the food items appropriately (e.g. Smith *et al.* 1989). In addition, when food is chopped or peeled, it is more susceptible to desiccation and loss of nutrients, especially vitamins (Lamikanra *et al.* 2005). Chopping food also increases the surface area available for exposure to bacteria and other contaminants.

So should zoos chop or peel food? Only when there is a good reason to do so; otherwise, the animals will almost certainly benefit more from receiving whole foods.

offered (for example, a mixture of fresh fruits and vegetables) and the animals are allowed to choose what they consume. (The opposite of cafeteria-style feeding is **complete feed-style feeding**, which is essentially the provision of a processed diet that meets the nutrient requirements of the animal, but does not offer any choice). But, as we have already seen in **section 12.1.3**, animals do not necessarily have nutritional wisdom and may not consume a balanced diet if food is presented in a free-choice CSF approach.

Some plant foodstuffs are also freely available within an enclosure because they grow there (for example, grass, other vegetation, fruit trees, etc.). In these instances, the issue may not be that food-stuffs need to be available to animals to eat, but rather the opposite—that the animals' access to the plants may sometimes need to be restricted. This can be for aesthetic reasons (to ensure that attractive trees and shrubs survive), or to limit consumption of potentially toxic plant matter (see **Box 12.1**).

How often should animals be fed?

Many zoo animals are fed once or twice a day (**Fig. 12.25**). But because animals in the wild often forage for a large part of the day, there is a widespread assumption that it is somehow 'better' to feed more often and that providing a greater number of smaller feeds throughout the day may be a useful form of **enrichment**, at least for some species (see **Chapter 8**).

12.7.2 Intake

It is important to know what foodstuffs animals like and dislike, because this will determine which foods they choose to eat first and which foods are likely to be monopolized by dominant animals. Also, if too much food (quantity) is provided, animals may choose to eat only favoured food items and leave behind those foods that they do not like. This can be very frustrating for keepers and zoo nutritionists who have put much effort into providing a nutritionally balanced diet.

Figure 12.25 A giant anteater *Myrmecophaga tridactyla* with a bowl of food, at Ramat Gan Zoo in Tel Aviv, Israel. In the wild, giant anteaters spend a large part of the day foraging for prey species, such as ants and termites. In zoos, giant anteaters are often fed a gruel-like diet containing a mix of foodstuffs, such as canned cat food and fruit, as well as insects, when available. (Photograph: Tibor Jäger, Zoological Center, Tel Aviv)

One solution to 'food favouritism' is to provide animals with a diet that has less daily variety, so that all animals will have access to, and indeed will have to eat, certain food items (or go hungry). At Johannesburg Zoo, for example, the animals may receive a lot of apples and no oranges at a feeding session; the next day, oranges will be provided, but no apples (ICEE 2007).

Alternatively, different foods can be mixed together, so that the animals cannot easily avoid consuming all the foodstuffs provided. This food-mixing method was adopted for a colony of Rodrigues fruit bats *Pteropus rodricensis* at Chester Zoo after it became apparent that a particular feeding presentation style used for the bats was having a deleterious impact on the health of the animals (Sanderson *et al.* 2004). The bats had been fed a diet comprising mashed-up food, combined with primate pellets for additional protein. Larger chunks of fruit were also provided on spikes, to provide feeding enrichment for the bats. Because of the perceived success of the feeding enrichment, and its attractive appearance in comparison with a 'mush' of fruit and pellets, keepers started to provide the primate pellets separately to the fruit when feeding the bats. However, the dry pellets on their own were not consumed by the bats, so keepers reduced the quantity of pellets provided.

In the following breeding season, mortality levels in the Rodrigues bat colony rose, with a disproportionate increase in mortality among female bats that had lactated the previous year. An investigation by the zoo veterinary staff and nutritionist found that the food presentation style, intended as enrichment, in fact allowed the bats to select a nutritionally deficient diet and this had affected lactating females in particular (as well as demonstrating that fruit bats do not appear to possess nutritional wisdom—see **section 12.1.3**). Once Chester Zoo returned to its previous feeding regime for the fruit bats, providing fruit and primate pellets mixed together, mortality levels fell and the bat population recovered.

Presentation style can also affect the nutritional composition of the diet fed. We have seen already that food that is left exposed to the elements (for example, in buckets without lids) can start to lose some of its nutrient content. Food that is scattered directly onto the ground can also undergo a change in nutrient value as a result of direct contact with the soil in an enclosure, and animals may also ingest soil with their food, particularly if the food (and soil) is moist. For example, iron intake can be increased if food comes into contact with iron-rich soil (McCormick *et al.* 2006); this change in iron intake may be valuable if iron is deficient in the diet, or undesirable in species at risk of **haemochromatosis**[28] (see **section 12.8.1**). Similarly, iron intake in zoo (and farm) animals can rise when water used to fill troughs, or for nipple feeders, is supplied via rusty pipes.

Carcass feeding

Supplying only meat to carnivorous zoo animals, such as storks, hawks, lions, and tigers, is not enough; carnivores need to be fed whole prey, including blood, guts, organs, fat, and bones (**Box 12.6**). This is important both to ensure that their nutritional requirements are met and to maintain good dental health. Carnivorous and piscivorous birds and mammals, for example, may become calcium deficient if they are fed only soft tissues and not bones (Howard and Allen 2007).

12.7.3 Other functions of feeding

In many instances, the impact of feeding zoo animals goes far beyond merely the provision of nutrients. Depending on how food is presented, feeding can facilitate husbandry, improve health, provide mental and physical exercise for the animals, and also have a considerable impact on the education of zoo visitors. For example, providing food at the end of the day may enable keepers to move animals between areas of their

---

[28] **Haemochromatosis** is the correct term for iron storage disease, not to be confused with **haemosiderosis**, which is increased iron storage in the body that is benign and does not cause disease.

Box 12.6 CARCASS FEEDING: WHAT TO FEED CARNIVORES INSTEAD OF LIVE PREY?

As mentioned in **section 12.3.1**, it is illegal in the UK to provide live vertebrate prey to carnivorous (and piscivorous) zoo animals, such as storks, hawks, lions, tigers, and snakes; neither is the feeding of live vertebrate prey routinely practised in zoos elsewhere around the world (see **Box 12.2**).

So what are the alternatives? The obvious alternative to providing live prey is to provide meat (that is, all or part of the body of a dead animal), but there are various forms that this 'meat' can take. At one end of the spectrum, meat fed to zoo animals can be in the form of a dead, but otherwise intact or whole, animal; this is generally referred to as 'carcass, or whole prey, feeding' (**Fig. 12.26**). At the other end of the spectrum, zoos can feed 'meat products', which may contain non-meat material such as cereals (much like commercial dog or cat food).

The advantages and disadvantages of feeding different types of meat to zoo animals have been the subject of considerable debate, centring on issues such as nutritional value, the impact on the health of the animals being fed, and the acceptability to zoo visitors of carcass feeding. In terms of the nutritional content of a carnivore's diet, we know that carnivorous animals in the wild generally eat much more than only the muscle on their prey; they may eat, and gain nutritional benefits from, the blood, guts, organs, bones, and hair/feathers of their prey. This could lead to the recommendation that zoo carnivores should be fed carcasses, because all these additional body parts would then be presented to the animals. But all the nutritional requirements of most carnivores can also be met by feeding meat products, because these products are specifically formulated to ensure that they contain all the necessary nutrients, including vitamins and minerals (which, in the case of vitamins in particular, can be lost during storage of carcasses). In fact, the ability to monitor an animal's nutritional intake when it is fed a formulated diet is easier than trying to quantify the nutritional composition of naturally occurring foods, which may vary in many ways and thus differ in their nutritional composition.

Carcasses may be undesirable foodstuffs in other ways: the fat content may be too high, or the carcass might be a vector for disease (for example, parasite transmission). Other health risks that have been suggested in relation to carcass

Figure 12.26 These photographs show zoo animals feeding on carcasses or whole prey. (a) The meerkat *Suricata suricatta* is feeding on a whole dead chick, supplied within a cardboard tube to provide feeding enrichment. (b) A tree boa *Corallus* sp. at Colchester Zoo in the UK, feeding on a whole dead rat. (Photographs: (a) Paignton Zoo Environmental Park, (b) Colchester Zoo)

feeding include gut impaction or obstruction, or gut perforation by bones. However, a recent survey of zoos worldwide shows that feeding carcasses does not increase the risk of health problems in zoo carnivores when compared with feeding commercial diets (Knight *et al.* 2005). Moreover, there are other data that associate the provision of carcasses, or meat on the bone (**Plate 12.1**), with health benefits to zoo carnivores, such as improved muscle and body condition, and oral health (Fitch and Fagan 1982; Bond and Lindburg 1990; Houts 1999).

Similarly, concerns that feeding carcasses may lead to increased aggression (if only one or two food items are provided for a social group of carnivores) are not supported by any firm scientific evidence. There is anecdotal evidence that carcass provision may strengthen social bonds in wolves (Ziegler 1995; Houts 1999) and bush dogs (Macdonald 1996). A study by Bond and Lindburg (1990) showed that carcass provision improved the appetites of captive cheetah, which fed for longer and also displayed species-characteristic possessive behaviour over their food, compared with their behaviour when fed commercial diets. Other studies have shown that carcass feeding, or the provision of meat on the bone, promotes natural foraging and food-processing behaviours, and can reduce the expression of **stereotypies** (e.g. Carlstead 1998; McPhee 2002; Bashaw *et al.* 2003).

These data suggest that zoos should provide carcasses, or at least meat on the bone, for their carnivores. However, a survey of zoos worldwide suggests that there are considerable regional variations in the type of meat provided for zoo carnivores (Knight *et al.* 2005) (**Fig. 12.27**). It would seem that, in US zoos, commercial 'meat diets' predominate, whereas carcass feeding is favoured elsewhere in the world. So if all the available evidence demonstrates that carcass provision does not negatively impact on animal health and is beneficial in terms of behavioural expression, why do zoos not universally implement this form of feeding?

It is possible that the ability to monitor the nutritional content of a carnivore's diet more carefully may bias a zoo towards choosing a commercial diet over carcass feeding. It has also been suggested that the logistics and regulations involved in sourcing, storing, and preparing meat may vary across regions, and that this may discourage zoos from providing carcasses. But it is the perceived views of zoo visitors that seem to be a key factor in determining whether or not zoos feed carcasses to their carnivores.

However, a survey of zoo visitors in the UK, Belgium, Australia, and New Zealand indicated that they would not object to seeing animals being fed carcasses (Melfi and Knight 2009). We await with interest data on the views of visitors to zoos in the USA; it is possible that the low rate of carcass feeding in US zoos is due to public objections (or the perception of public objections) to this practice.
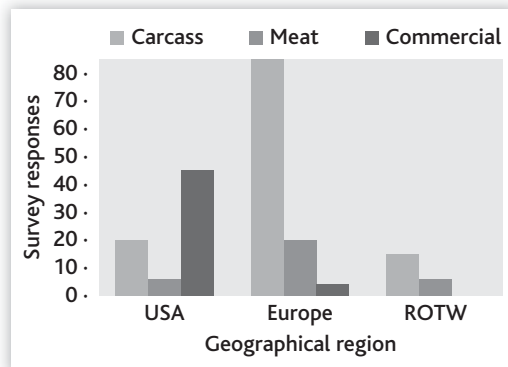
Figure 12.27 This graph shows regional differences in the feeding of carcasses (whole dead prey), meat, and commercial meat diets. (From Knight *et al.* (2005))

enclosure—notably, from outside areas to inside areas, when they want animals to be in secure indoor accommodation overnight.

There are also many ways in which food can be presented to zoo animals that can be considered enriching. In **Chapter 8**, we saw that one of the primary goals of much enrichment used for zoo animals is to boost the amount of time the animals spend foraging, so that their **activity budget** more closely resembles that of their wild

conspecifics. For wild birds in particular, obtaining food is often their main activity, and in the winter months non-migratory bird species can spend more than 80 per cent of daylight hours foraging (Klasing 1998). Replicating this level of activity in captive birds poses a particular challenge for zoos, but the use of feeding enrichment can go some of the way towards providing a solution (e.g. Vargas-Ashby and Pankhurst 2007).

Finally, we need to make some mention of the ubiquitous use of feeding time at the zoo as a visitor attraction. Most zoos make a point of advertising to their visitors when they are going to feed certain species within their collection. This provides an almost guaranteed opportunity for many visitors to see animals that usually hide away, or to see animals doing something that they usually are not, or to learn more about the animals from educational presentations given during feeding time, or a combination of all these.

12.8 Nutritional problems

Zoo animals can experience a variety of nutritional problems, from the accidental ingestion of litter or deliberate feeding of unsuitable food items by zoo visitors, to obesity or **malnutrition**. Vitamin and mineral deficiencies can lead to health problems, as can these substances in excess in the diet. Species categorized as browsers rather than grazers (for example, moose, giraffe, tapirs, and black rhinoceros *Diceros bicornis*) are often regarded as difficult to keep and to breed in captivity, and seem to be more susceptible to diet-related health disorders (Clauss and Dierenfeld 2007).

Nutritional diseases have been mentioned briefly in **Chapter 11**, but two diet-related diseases that give cause for concern in many zoos and which we will now look at in more depth are metabolic bone diseases and iron storage disease.

12.8.1 Nutritional diseases

Metabolic bone diseases

As Ullrey (2003) points out, the term 'metabolic bone disease (MBD)' is often used as though it is only one disease, but, in fact, there are several different bone diseases[29] or disorders that can arise when something goes wrong with an animal's metabolism (**Fig. 12.28**). Bones can lose density or bone mineral (osteopenia or, in severe cases, osteoporosis) or can become softened (rickets or osteomalacia)[30].

Rickets, with its characteristic bowing of the long bones such as the femur or humerus, is perhaps the best-known bone disorder and can occur in a wide range of taxa. In fact, rickets and osteomalacia are essentially the same disorder. The term 'rickets' is generally used for the disease in young animals, when the bones are still forming. Both disorders are associated primarily with vitamin D deficiency, but can also occur as a result of insufficient calcium or phosphorus in the diet.

Figure 12.28 Reptiles, such as this green iguana *Iguana iguana*, require a source of UVB light in order to be able to metabolize calcium properly. The tail of this animal is permanently distorted as a result of metabolic bone disease due to an inadequate diet earlier in its life. (Photograph: Sheila Pankhurst)

[29] It is not only bones that can be affected by MBD; tortoises, for example, can show MBD in carapace ('shell') development (Hatt 2007).

[30] Osteopenia is bone mineral density that is lower than would be considered normal, and can be a precursor to osteoporosis, which is a disease of bone that can lead to an increased risk of fractures. Osteomalacia is a softening of the bones caused when there is a deficiency of minerals such as calcium and phosphorus in the diet (or the animal is not able to metabolize these efficiently).

All the MBDs mentioned here can arise as a result of poor nutrition and dietary deficiencies although, in several cases, there is also a genetic component to the disease. Bone disorders are of serious concern to zoo vets and nutritionists, because the damage to the bone is often irreversible and can sometimes be fatal. Fidgett and Dierenfeld (2007), for example, report on the potential for the rapid onset of severe MBD in stork species when there is a calcium deficiency in the diet of these birds.

There is a complex relationship between vitamin D_3, ultraviolet B light (UVB), calcium, and phosphorus in the body. A number of exotic species lack the ability to synthesize vitamin D_3 in the body and dietary deficiencies in this vitamin can lead to bone disorders such as rickets. Other animals, including reptiles such as the green iguana, require a source of UVB light in order to be able to metabolize calcium properly (McWilliams 2005a). For example, captive Komodo dragons *Varanus komodoensis* kept in indoor facilities in zoos showed significantly lower levels of vitamin D_3 than those of either wild dragons or captive dragons kept in exhibits with outdoor access (Gillespie *et al.* 2001). This study demonstrated that the implementation of corrective measures (such as the use of UV lamps, direct exposure to sunshine, or the installation of UV-permeable skylights) could bring vitamin D_3 levels in indoor-housed animals up to levels that were comparable with those found in wild animals.

There are two useful papers on calcium homeostasis in Volume 39 of the *International Zoo Yearbook*, with feeding and lighting recommendations for lizards and freshwater turtles, respectively (McWilliams 2005a; 2005b). The Nutrition Advisory Group (NAG) of EAZA also provides a fact sheet (Fact Sheet 002) entitled *Vitamin D and Ultraviolet Radiation: Meeting Lighting Needs for Captive Animals* (Bernard 1997).

Figure 12.29 Provision of an adequate supply of browse is particularly important for the health of black rhinoceros *Diceros bicornis* in captivity (Clauss and Hatt 2006). (Photograph: Kirsten Pullen)

Iron storage disease

Iron storage disease, or haemochromatosis, is the term used to describe the **pathology** associated with deposits of iron in the body tissue, most often in the liver (other organs such as the kidneys and heart may also be affected). Iron storage disease has a known genetic basis in humans, and a genetic susceptibility is also indicated in a number of exotic species (for example, the mynah bird *Gracula religiosa* (Mete *et al.* 2003)). Among mammals, many primate species, such as lemurs (Spelman *et al.* 1989), are susceptible to haemochromatosis. Black rhinoceros *Diceros bicornis* and Sumatran rhinoceros *Didermocerus sumatrensis* are susceptible to iron storage disease (Dierenfeld *et al.* 2005) (**Fig. 12.29**), although **haemosiderosis**[31] can occur in black rhinoceros without any **clinical signs** of disease. There is also increasing evidence that iron storage disease is a contributing factor in **morbidity** and failure to breed in zoos in a number of exotic bird species (Taylor 1984; Cork 2000; Sheppard and Dierenfeld 2002).

Iron storage (particularly in the liver) appears to be a problem for those rhinoceros species that are browsers rather than grazers (Clauss and Hatt 2006). Black rhinoceros feed mainly on browse in the wild, but in captivity are often managed

---

[31] **Haemosiderosis** refers to the accumulation of iron in the body. This can be a precursor to haemochromatosis, but may not have any pathological effects.

Figure 12.30 The most common group of birds to suffer from haemochromatosis, or iron storage disease, are the toucans and hornbills (such as this rhinoceros hornbill *Buceros rhinoceros*), and their relatives. (Photograph: Paignton Zoo Environmental Park).

as grazers, with a diet supplemented with high-energy concentrates. Overfeeding of black rhinos appears to be a contributing factor to iron storage disease and can also lead to obesity. Provision of browse and adequate roughage in the diet is also very important for the health of these animals in captivity (Clauss and Hatt 2006).

Haemochromatosis is well documented in captive hornbills (**Fig. 12.30**), and also in toucans, toucanets, and their relatives. The disease is also often found in some mynah birds, tanagers, and birds of paradise in captivity, but not in these species in the wild (Klasing 1998). Rather puzzlingly, many of the susceptible bird species are frugivores, but fruit is generally a poor source of iron. Consumption of ascorbic acid (vitamin C), however, increases the body's ability to take up iron, so citrus fruits and other foods high in vitamin C are not always recommended for bird species that may be prone to iron storage disease, or are fed separately (Sheppard and Dierenfeld 2002).

12.8.2 Nutritional disorders

The two main nutrition-related disorders are obesity and malnutrition. Malnutrition is not due to a shortage of food *per se*, but rather to a deficiency or deficiencies in nutrients in the diet.

Various deficiencies, particularly of vitamins, can give rise to disease.

Malnutrition

Malnutrition arises because of the lack of a specific nutrient (or nutrients) in the diet: the total quantity of food consumed by the animal may be adequate, but an essential component (such as a vitamin or mineral) is lacking. Nearly all macro-minerals and vitamins can cause health problems when deficient in the diet (and also when present in excess—see later). We have provided only a few selected examples here.

For general information about vitamin and mineral deficiencies, and their impact on growth and health, we recommend McDowell (2000; 2003) for mammals and Klasing (1998) for birds. Chapter 5 of McDonald *et al.* (2011) also provides a useful account of vitamins and nutrition, and includes a table summarizing the disorders caused by vitamin deficiencies. Information on vitamin and mineral deficiencies in non-mammalian and non-avian taxa is harder to come by, and is rather more scattered throughout the literature, although Fowler and Miller (see in particular the fourth edition—Fowler and Miller (1999)) is a good starting point.

Vitamin deficiencies

Examples of vitamin deficiencies that are of particular concern in zoos include deficiencies in vitamins A, C, and E. Vitamin A is important because of its role in immune system function; a deficiency of this vitamin can make animals much more susceptible to infection. Several studies have reported that death from infection can occur well before signs of a vitamin A deficiency become apparent (for example, in poultry, see Sklan *et al.* (1994)).

Vitamin C deficiency can present a problem in non-human primates, particularly if commercial feeds are stored for long periods of time, because levels of this vitamin decrease markedly in foodstuffs after more than a few months in storage (Lamikanra *et al.* 2005).

Vitamin E is believed to play an important role in the function of cell membranes. As we have already seen in this chapter, vitamin E is readily lost from fish during storage and, for this reason, it is often given as a routine supplement (along with

thiamine or vitamin B_1) to fish-eating mammals and birds. Vitamin E supplements (by injection or as an additive to food) are also sometimes given to exotic animals in captivity prior to capture and handling, in an attempt to reduce **capture myopathy**[32], although the evidence to support the value of this practice is mixed (e.g. Graffam *et al.* 1995).

Mineral deficiencies

Mineral deficiencies are rather like the diseases of concern that we discussed in **Chapter 11** and will vary from collection to collection. For example, in some areas, the pasture on which grazing animals feed can be deficient in selenium,[33] because of the mineral composition of the soil. This effect can be highly localized, but can have a major impact upon hoof growth and other aspects of health.

The situation is further complicated by interrelationships between minerals and other nutrients. Selenium, for example, works in conjunction with vitamin E as an antioxidant within the body and, to some extent, these two substances can compensate for each other (McDowell 2003), so that animals with an adequate intake of vitamin E are better able to cope with very low levels of selenium in their diet, and vice versa.

The signs of mineral deficiencies in animals are not always obvious, and can be similar to the signs of other diseases and disorders. So-called 'wasting diseases' or 'wasting syndromes' (in which an animal shows progressive loss of weight over a period of time) can be related to mineral deficiencies, but can also be due to infectious agents.

Animals suffering from a mineral deficiency may also exhibit **pica** which, in livestock, is a term generally used to refer to animals eating items not usually found in their diet (e.g. Golub *et al.* 1990). Bone or antler eating can indicate a deficiency in calcium or phosphorus in the diet. This behaviour, known as osteophagia, is frequently observed in giraffes (Bredin *et al.* 2008). The skeleton in

giraffes has a particularly high calcium content (Mitchell *et al.* 2006); giraffes normally meet their requirement for calcium by consuming calcium-rich dicotyledonous browse (**Plate 12.2**), which is one reason why it is important for zoos to provide adequate browse for these animals.

A deficiency in zinc in captive birds fed a grain-based diet is not uncommon, and can have adverse effects on growth and egg production (Klasing 1998). For example, zinc deficiency in ducks can lead to the development of dermatitis on the webs of the feet and/or the fraying of new feathers after moulting (McDowell 2003).

Toxicity

As well as health problems caused by nutritional deficiencies, an excess of a particular nutrient or substance can also lead to diseases and disorders that can, in some cases, be fatal. As already outlined in **section 12.1.3** and **Box 12.1**, many plant species are poisonous to the animals that eat them, or may attempt to eat them. Zinc toxicity has been reported in captive birds that have gnawed at the galvanized wire of their cages (on fatalities in **psittacines**, for example, see Howard (1992)).

Obesity

Body weight is often used by keepers and vets as a measure of health in zoo animals, with comparisons with data from wild animals of the same species (e.g. Terranova and Coffman 1997). In ruffed lemurs, for example, Schwitzer and Kaumanns (2001) looked at a sample of forty-three animals from thirteen European zoos, and found that more than 46 per cent of individuals were obese.

In general, obesity is a much greater nutritional problem in zoos than malnutrition. This is for a variety of reasons.

- The legislative framework in the UK does not allow zoos to withhold food (this is set out in

---

[32] **Myopathy** refers to the build-up of lactic acid in muscles; this can cause stiffness, paralysis, or even death. **Capture myopathy** has been reported in a wide range of taxa and can cause death almost immediately, or up to a few weeks later.

[33] The mineral selenium can cause health problems in animals both when it is deficient in the diet and when it is over-abundant. Selenium toxicity can cause animals to lose hair or even hooves (McDowell 2003).

the SSSZMP (Defra 2012a); see **section 12.3.1**), so there is a relatively high **plane of nutrition** for most zoo animals.

- In captivity, animals may not have as many opportunities for activity as they would in the wild and their motivation to exercise may be reduced if they are overfed.

- Obesity can also arise in dominant animals in a group if these individuals are highly successful at obtaining food intended for more than one animal. Zoos may deliberately provide surplus food for group-housed animals, to ensure that subordinate animals receive enough food, but this can result in dominant animals consuming much more food than they need and becoming obese. (The converse is also true: subordinate animals may not get their fair share of food and can lose condition.)

- Another factor that can contribute to obesity in zoo animals is the feeding of energy-dense commercial feeds; feeds developed for livestock will be formulated for 'high production', or rapid weight gain, and may not be appropriate for zoo animals.

- Zoo diets may not show the seasonal variation with which animals are adapted to cope in the wild; many animals are physiologically adapted to lay down fat reserves before the winter, but these animals can then gain excess weight if their food supply is not reduced in the winter months.

- Finally, keepers may overfeed animals in the same way that some (misguided) pet owners overfeed their pets.

Obesity is of concern to zoos because it can lead to other health problems, such as reduced **fertility** or limb problems. In Indian rhinoceros *Rhinoceros unicornis*, for example, obesity appears to be linked to other health problems such as foot disorders (Clauss *et al.* 2005). Obesity is also linked to the development of diabetes in captive primates (for example, in orang-utans *Pongo pygmaeus* (Dierenfeld 1997b)).

Reproductive disorders

Nutritional deficiencies can have a profound effect on reproduction. As we saw in the previous section, there is evidence that iron storage disease is a contributing factor in the failure of a number of exotic bird species to breed in zoos (Taylor 1984; Cork 2000; Sheppard and Dierenfeld 2002). We also saw in **Chapter 9** that factors such as maternal nutrition can have a significant influence on sex ratio (e.g. Kilner 1998). Overfeeding can also lead to the development of large fetuses in vertebrates which, in turn, can lead to health problems at parturition or egg-laying.

A number of mineral and vitamin deficiencies have been documented to have an adverse effect on reproduction. In livestock, for example, a deficiency in vitamin A can cause congenital abnormalities in fetuses, and a copper deficiency leads to reduced egg production and 'hatchability' in poultry (McDonald *et al.* 2011). Less is known about the effects of nutritional deficiencies on reproduction in exotic animals, but there is still a body of data demonstrating that poor nutrition can have an adverse effect on reproduction (for reviews, see Allen and Ullrey 2004; Howard and Allen 2007).

Howard and Allen (2007), for example, have reviewed nutritional factors affecting semen quality in non-domestic felids, and point out a recurring link between poor diets and poor reproduction. This is highlighted in a study of South American felids in captivity by Swanson *et al.* (2003) who found that, in a sample of 185 adult male cats from eight species (including ocelots *Leopardus pardalis* and jaguar *Panthera onca*) kept in forty-four zoos in Latin America, only around a third of the cats received nutritionally adequate diets and only 20 per cent of the males were classified as 'proven breeders'.

Among birds, Fidgett and Dierenfeld (2007), in a recent review of minerals and nutrition in stork species, concluded that nutritional factors are likely to be a key component of successful captive breeding of these carnivorous birds.

Dental disorders

As well as the risk of nutritional diseases or disorders developing, provision of an inappropriate diet can have serious consequences for the oral health of zoo animals. The consistency of food has an effect on the rate at which dental plaques form, and a diet composed largely of soft foods will lead to greater plaque formation than will a diet of hard foods (Braswell 1991). This can be a particular problem for carnivores fed only on meat or commercial meat diets, rather than on carcasses or meat on the bone.

Diets may also need to be adapted for elderly zoo animals that have lost teeth or have other dental problems.

Summary

• The aim of 'captive feeding' in zoos is to provide optimal nutrition.

• Legislation governing zoo animal feeding and nutrition requires that zoos provide sufficient food and water, but the provision of an optimal diet falls largely outside the legislative framework of most countries (although within the UK, the SSSMZP provide quite detailed recommendations on zoo animal feeding and nutrition).

• Zoos cannot hope to match exactly the wild diets of all the animals in their care, but they can try to match the nutritional content of wild diets.

• Much of what we know about the detailed nutritional requirements of animals is based on models of domestic animals, such as cattle, sheep, poultry, and cats and dogs, but these nutritional models may not always be appropriate for zoo animals.

• Zoos today have access to an increasing range of guidelines and tools to help them to develop diets providing optimum nutrition for their animals. Foremost among these tools is the nutritional software package and database, Zootrition™.

• Nutrition can have profound effects on other aspects of an animal's life history, such as its health, physical and mental development, reproduction, and mortality.

• Obesity is a greater problem in zoos than malnutrition (by law, zoos must provide sufficient food for their animals); nutritional diseases of particular concern to zoos include metabolic bone disorders and iron storage disease, or haemochromatosis.

Questions and discussion topics

1. Do animals have 'nutritional wisdom'?
2. What is Zootrition™, and how can it be used by zoos to improve the health and welfare of their animals?
3. What are the main nutritional problems and disorders that are found in animals in zoos, and what steps can be taken by zoos to prevent these occurring?
4. Which broad group of animals poses a greater challenge for zoos in terms of 'captive feeding'—carnivores or herbivores?

Further reading

For anyone wanting to learn more about the basic principles of animal nutrition, we highly recommend McDonald *et al.*'s comprehensive text, *Animal Nutrition* (2011), now in its seventh edition. Although largely about mammalian livestock species, this book provides much useful general information on nutrients and digestion, and has chapters with titles such as 'Hay, artificially dried forages, straws and chaff'. The diagrams of gastrointestinal tract structure in this chapter are all taken from Stevens and Hume (2004); their book *Comparative Physiology of the Vertebrate Digestive System* is a very useful source of information on digestive physiology across all vertebrate taxa.

In 1999, Edinburgh Zoo hosted a symposium on *Nutrition of Wild and Captive Wild Animals*.

The plenary speaker at this meeting was Dr Ellen Dierenfeld, then at the Wildlife Conservation Society/Bronx Zoo, who gave a lecture on the historical perspective to the developing science of zoo animal nutrition. Her lecture is published as a paper in the *Proceedings of the Nutrition Society* (Dierenfeld 1997a) and it is well worth getting hold of a copy, not least for the comprehensive reference list.

Proceedings of the first European Zoo Nutrition Conference, held in the Netherlands in 1999, have been published in book form under the title *Zoo Animal Nutrition* (Nijboer and Hatt 2000). Volumes II and III of *Zoo Animal Nutrition* followed in 2003 and 2006, respectively, with Dr Andrea Fidgett (nutritionist at Chester Zoo) as the leading editor (Fidgett *et al.* 2003; 2006); Volume IV, edited by Clauss and Fidgett, was published in 2009. These useful books, all of which can be ordered from the Natural History Book Service website (**http://www.nhbs.com**) contain research papers and reviews on a wide range of topics relating to zoo animal nutrition. Andrea Fidgett is also a co-author, with Dr Amy Plowman from Paignton Zoo Environmental Park, of the BIAZA *Zoo Research Guidelines on Nutrition and Diet Evaluation* (Fidgett and Plowman 2009), available from the BIAZA website.

Information about feeding browse in zoos can be obtained from BIAZA (Plowman and Turner's browse database is available on CD), and from the Dutch and Belgian zookeepers' association (their guide is available in Dutch and English, for €10 plus postage, from D.Blomojous@Rotterdamzoo.nl). Kirk Baer *et al.* (2010) provide a short list of the nutrient composition of some of the browse species (including acacia, beech, *Ficus* spp., and alder) commonly fed to zoo herbivores in the USA and Canada.

Five chapters in the excellent and detailed first edition of the book *Wild Mammals in Captivity*, edited by Devra Kleiman and her colleagues, are devoted to the nutrition of mammals in zoos (Kleiman *et al.* 1996). For Australian mammals, we recommend Stephen Jackson's book, *Australian Mammals: Biology and Captive Management* (Jackson 2010).

Recommended texts that consider taxa other than the mammals include Klasing's *Comparative Avian Nutrition* (1998), Robbins' *Wildlife Feeding and Nutrition* (1993), Lovell's *Nutrition and Feeding of Fish* (1998), and (also on fish) Halver and Hardy's *Fish Nutrition* (2002).

Several editions of Fowler and Miller provide detailed accounts of nutrition-related diseases and disorders, across a wide range of taxa (including fish); for example, the fourth and sixth editions (Fowler and Miller 1999; 2007) contain a great deal of information about the impact on health of various vitamin and mineral deficiencies in the diet of wild animals in captivity.

Finally, three volumes of the *International Zoo Yearbook* have zoo animal nutrition as their main theme: Volume 6 (published in 1966), Volume 16 (published in 1976), and Volume 39 (published in 2005).

Websites and other resources

Guidelines and other sources of information about zoo animal nutrition have already been discussed in some detail in **section 12.3.3**; we particularly recommend the nutrition pages on the EAZA website (**http://www.eaza.net**) as a first port of call.

In addition to these guidelines and databases such as Zootrition™, another widely used source of information is the series of publications from the National Research Council (NRC) of the US National Academy of Sciences. The NRC publications are consulted not only within zoos, but also by livestock farmers, laboratory animal managers, and the pet food industry. There is more information about NRC nutrient requirement publications in **Box 12.3**.

Also from the USA, the US Department of Agriculture (USDA) has an extensive searchable database of nutrient values for a very wide range of human foodstuffs, which is available online at **http://www.ars.usda.gov**.

Finally, the website of the Comparative Nutrition Society (**http://www.cnsweb.org**) has details of published proceedings of the meetings of the Society. (The interests of the Society are wide-ranging, and span nutrition, physiology, and biochemistry across all animal taxa.)

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.

http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Chapter 13
People in zoos

Zoos are not only full of animals, they are also full of people. Some of these people work in the zoo; they may, for example, be keepers, managers, researchers, or volunteers. But most are visitors, ordinary members of the public who come to the zoo to see the animals. The money that these people bring to the zoo constitutes a major source of funding to support the zoo and its conservation activities, so it is important for the zoo to know who these people are and why they come, and also to ensure that they have an enjoyable and rewarding experience. And since most zoos aim to raise awareness and increase knowledge of animals and conservation in these visitors, it is also important to know whether and how well they do this.

At the same time, the sheer number of visitors, several thousand of whom may pass through on a typical day, and the continual presence of familiar people like keepers, means that humans are a significant part of the zoo animal's environment, and are likely to have some impact on the behaviour and welfare of the animal. While this influence may sometimes be positive or neutral, it can also be negative, and detrimental to the welfare of the animals, so we need to measure the extent and type of that influence. Reciprocally, the animals are likely to have some impact on the humans, so we can imagine a sort of 'zone of contact' within which humans and animals come into sufficient proximity to be able to influence each others' behaviours.

In all these cases, we can refer, in a general way, to 'human–animal interactions', using the word 'interaction' in the sense that it was used by Estep and Hetts (1992) to mean some kind of behaviour performed by one individual that influences the behaviour of another, thus making it a kind of communication. This type of interaction can be used by the zoo to increase the public's knowledge of, and concern for, the animals and their conservation, while at the same time giving them an enjoyable experience. The ideal is to create a zoo environment in which the animals' and humans' experience of each other is as positive as possible.

In this chapter, we will consider what we know about people in the zoo, and examine some of the ways in which the animals and humans influence each other. We will cover the following topics.

Therefore in this chapter we are looking not only at human–animal interactions in the zoo, but also, a little more widely, at the consequences of this for people's experiences of the zoo.

Related topics to do with the interface between the public, the keepers, and the animals are considered in boxes throughout the chapter.

13.1 Zoo visitors: what do we know about them?

It is self-evident that zoo visitors are fundamentally important to the operation and success of zoos, in terms of their stated objectives. Visitors are the targets of zoo educational initiatives and are, ultimately, the primary funding source for any conservation work that zoos do. So we would expect zoos to find ways of maximizing their attractiveness to visitors, and to provide an experience that is consistent with welfare, educational, and conservation priorities, but is also enjoyable for the visitors.

13.1.1 Who visits zoos?

Zoos are a major attraction. A survey by WAZA has shown that more than 700 million people visit zoos and aquariums worldwide each year (Gusset and Dick 2011) (**Fig. 13.1**)—an astonishing figure, given the number and variety of other attractions which zoos compete with.

In the face of that competition, zoos appear to be holding their own extremely well (Turley 1999); indeed, in the UK and the USA, zoo attendances have been increasing over the past few decades (Davey 2007a).[1] A socio-economic survey undertaken for BIAZA showed an annual UK zoo attendance of 23.7 million in 2008, representing a third of the UK population (BIAZA 2010a); it also showed that zoos were the most popular destination of choice for children after the seaside. And such figures are not only seen in UK zoos; the zoos in Copenhagen and Rotterdam attracted

[1] Although Davey's analysis shows that elsewhere there has been a slight decline in zoo attendance since the 1960s.

Figure 13.1 Zoos worldwide are popular venues for recreation and education, as this photograph of a queue of visitors shows. (Photograph: Tibor Jäger, Zoological Center Tel Aviv–Ramat Gan, Israel)

more visitors than any other urban attractions in those cities during the early 1990s (Mason 2000). In Australia, 5.7 million people, representing 35.6 per cent of the Australian population aged 15 and over, visited a zoo or aquarium in the year prior to the survey (Linke and Winter 2011).

Therefore we may well ask who these visitors are, what they do when they are at the zoo, and what they think of their experience. However, there is not as much information available as we would like in order to answer these questions. What information there is may be difficult to locate, because it appears in unpublished reports with limited circulation, or because it is submerged in the tourism literature, or in a wider study that treats the zoo as a kind of museum[2] (e.g. Bitgood 2002), and thus appears in the museum, rather than the zoo, literature (but see Schramm (2011) for a comprehensive bibliography of visitor studies).

No clear overall patterns have emerged from these studies, but, in general, it appears that there are no particular distinguishing characteristics that define the zoo visitor, although it has been suggested that the most common visitors are families with young children (Cain and Meritt 2008). This is probably encouraging, because it implies that all sections of society are likely to visit zoos and therefore be exposed to animals and conservation messages. Kreger and Mench (1995) have pointed out that people are actually highly motivated to view animals and that the opportunities for interaction that are afforded by zoos (for example, shows, demonstrations, children's zoos, etc.) can have a profound impact on education and conservation awareness in people (**Fig. 13.2**). However, studies of visitor behaviour sometimes show that zoogoers' conversations are not very much about the animals (Altman 1998), although talking about the animals can be used by people as a way of facilitating social interaction (Clayton et al. 2009).

Figure 13.2 Animal demonstrations and shows, such as this bird show at Taronga Zoo, can give people an immediate and positive experience of animals which might have an impact on their knowledge and conservation awareness. (Photograph: Geoff Hosey)

Thus, it appears that people visit zoos for a variety of reasons, not all of which are to do with animals (there is more on this in **section 6.1.3**). For some, zoo visiting may be a social event (Morgan and Hodgkinson 1999) and more time is spent in conversation than in looking at animals; for others, the experience of encountering live animals can be an emotional event (Myers et al. 2004, Clayton et al. 2009).[3] The other side of the coin is that the animals are a sufficient distraction that other things, like learning about them, do not take place (Smith et al. 2011), and in the case of some animals (snakes are not universally liked by all zoo visitors) the human response might be disgust rather than more positive feelings (Cushing and Markwell 2011).

13.1.2 What do zoo visitors do at the zoo?

Several studies have observed the way in which people behave in zoos and have shown phenomena such as a tendency to follow routes involving right turns, and a decline in interest through the day, which are similar to the way visitors behave

---

[2] Indeed, it has been said that the zoo *is* a kind of museum, differing from other museums only in that its exhibits are alive (Mason 2000).

[3] The emotional dimension of contact with wild animals is expressed in Wilson's (1984) 'biophilia' hypothesis, that humans have an '*innate tendency to affiliate with life*'.

in other attractions such as museums (Davey 2006a). Probably the most consistent observation that has come out of these studies is that people spend remarkably small amounts of time actually looking at the exhibits.

In one study, Marcellini and Jenssen (1988) observed nearly 600 people visiting the reptile house at the National Zoological Park in Washington, DC. They tracked these people through the house, recording how long they spent looking at each exhibit. The mean time spent in the reptile house per visitor was only 14.7 minutes, of which 8.1 minutes were spent looking at the exhibits rather than walking around. This same study found clear differences in the time spent looking at different kinds of animal in the reptile house, with crocodilians being watched for longest and amphibians for the least amount of time (**Fig. 13.3**). Similar results were found at the Australian Reptile Park, where the average time spent in the Lost World of Reptiles exhibit was 12 minutes (Markwell and Cushing 2009). And it isn't just reptiles that generate short viewing times. Visitors to an immersive exhibit, the Regenstein African Journey at Lincoln Park Zoo, Chicago, had a median visit time of 11.08 minutes, of which 41 per cent was spent looking at the animals and

9 per cent engaged with the interpretive elements (Ross and Gillespie 2009); at the same zoo visitors spent an average of 8 minutes 36 seconds in the Great Ape House, and only 46 seconds engaging with interpretive materials (Ross and Lukas 2005). So, what do people like seeing at the zoo, and what might make them spend longer at each exhibit? In the study by Marcellini and Jenssen (1988) mentioned above, people spent longer looking at the relatively larger animals. This relationship—that larger animals are, in some way, more attractive or popular than small animals—has been claimed for other zoos and other kinds of animal as well (Ward *et al*. 1998), although it is quite possible that it depends very much on how popularity is measured. In the study by Ward *et al*. (1998), popularity was measured as the proportion of visitors at an exhibit who spend more than ten seconds looking at it. However, Balmford and colleagues (Balmford *et al*. 1996; Balmford 2000) used a measure of the proportion of people passing an exhibit who actually looked at it rather than simply walking past, and found no relationship between popularity and body size of animals. A study at Recife Zoo in Brazil also found no relationship between popularity of a number of mammalian exhibits and a variety of exhibit features, including body size
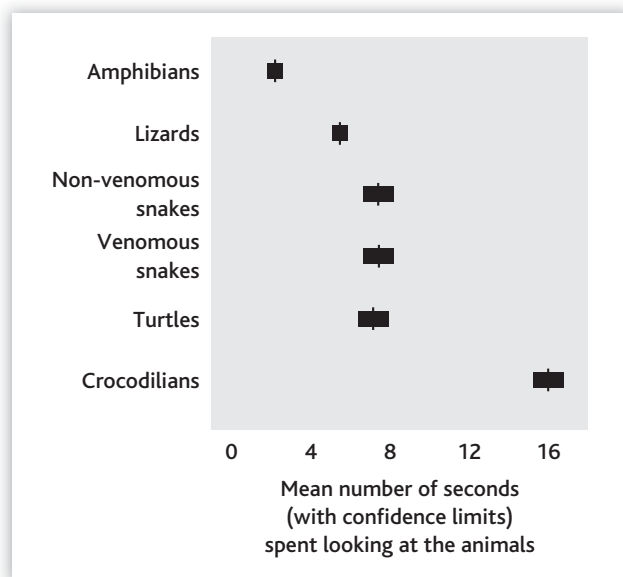
Figure 13.3 Visitors to the Reptile House at the Smithsonian's National Zoo in Washington, DC, spent most of their time looking at large-bodied species such as crocodilians and least time looking at small animals such as amphibians, but did not actually spend very long looking at any of them. (From Marcellini and Jenssen 1988)

and whether the species was exotic or native (da Silva and da Silva 2007). Body size does appear to be important, but popularity also seems to be based on other factors, notably taxonomy, with mammals being more popular than other groups (Moss and Esson 2010). In a somewhat different approach, Whitworth (2012) used questionnaires on people who were not at a zoo to gain an index of the popularity of different kinds of animals, and then used these to predict the popularity of different UK zoos, based on their species holdings. He found that these predicted popularity ratings[4] did indeed correlate with visitor numbers.

Another factor that might influence how long visitors spend at an enclosure is the visibility of the animals. At Zoo Atlanta, Georgia, visitors complained about difficulties in seeing tigers in a **naturalistic enclosure**, so signs were put up to point out to visitors where the cats were likely to be. Nonetheless, visitors generally did not use the signs, or even read them, and still came away thinking that they could not see the tigers (Bashaw and Maple 2001). At Disney's Animal Kingdom, Florida, the visibility of the animals is routinely monitored, and if it falls below a certain level for a particular animal, procedures are tried out which do not adversely affect the welfare of the animal, but are aimed at making it more visible, such as focusing enrichment (Kuhar, *et al.* 2010).

For a discussion of visitor behaviours in zoos outside Europe, North America, and Australia, see **Box 13.1**.

Visitor attendance times can be increased if the exhibits are more active or if they involve the public more. For example, attendance time at an otter exhibit at Zoo Atlanta was greater for animal training sessions than when the public only passively observed (Anderson *et al.* 2003). Similarly, unobtrusive video recording of visitors at zoo talks showed that people were more attentive if they had a good view of the speaker and the animals, and when the animals were active (Moss *et al.* 2010).

People particularly like to see active animals, as has been demonstrated with small felids (Margulis *et al.* 2003) (**Fig. 13.4**) and free-range tamarins (Price *et al.* 1994).

13.1.3 How do zoo visitors perceive the animals?

Valuable information can be obtained by watching what zoo visitors do and measuring how they spend their time while they are in the zoo. However, to understand their perceptions, attitudes, and quality of experience, it is usually necessary to use a questionnaire-based, rather than an observational, approach. Several studies have adopted this sort of approach both to find out about people's perceptions of zoo animals in general, and to evaluate whether various welfare, education, and conservation initiatives have helped to make people's attitudes more positive.

One of the earliest attempts to measure public perceptions of zoo animals was a study by Rhoads and Goldsworthy (1979), in which subjects were asked to rate pictures of animals in three different settings in terms of adjectives such as 'freedom', 'happiness', 'loneliness', 'dignity', 'friendliness', and 'naturalness'. Across several animal species, there were more negative ratings of pictures of caged zoo animals compared with 'semi-natural' (but still zoo) and 'natural'. Because the subjects were first-year psychology undergraduates[5] and they were rating pictures rather than real animals, it is not easy to generalize these results to the visiting public as a whole. Other studies, such as that by Finlay *et al.* (1988), have used similar methodology and a similar cohort of subjects, and have obtained similar results.

In contrast, Reade and Waran (1996) interviewed zoo visitors within the zoo and compared them with a control group of people interviewed in the street. They found that, although there were negative perceptions of zoo animals (for example,

---

[4] Amongst mammals the highest and lowest predicted popularity ratings were for primates and hippopotamus respectively; for birds it was parrots and frogmouths, and for herps it was iguanas and caecilians respectively.

[5] Psychology undergraduates are routinely used in psychological research, with the result that we probably know more about them than most other groups of people.

Box 13.1 VISITOR BEHAVIOURS AND PREFERENCES IN THE ZOO: THE VIEW FROM ASIA

The majority of studies of human behaviour in zoos, and how it impacts on the behaviour and welfare of the animals, have been undertaken in zoos in Europe, North America, and Australia. Yet it is very likely that there will be strong cultural differences among zoo visitors in different parts of the world, and that these differences may affect how visitors perceive and behave towards the animals. Few studies have looked at this aspect of zoo biology, but there are some recent studies that have investigated the extent to which zoo visitors in Asian zoos are similar to those in Europe and North America.

Firstly, Mallapur *et al.* (2005) investigated the effects of zoo visitors on lion-tailed macaques *Macaca silenus* in eight different zoos across India. The results were similar to those seen with macaques in Western zoos, in that abnormal and aggressive behaviours increased when visitors were present, and the animals appeared to be stressed by the visitors. Moreover, the increase in these behaviours was quite large in comparison with many of the European/North American studies (20 per cent more **abnormal behaviour** as a short-term effect and 30 per cent as a long-term effect). As the authors point out, there are few well-established conservation and welfare awareness programmes in Indian zoos, and consequently it is more common for animals to experience high levels of disturbance (such as shouting, teasing, feeding, and even physical harm) from zoo visitors. In a further study, however, Mallapur *et al.* (2008) found that visitors at three Indian zoos did know more about these macaques than the general public, and in two of those zoos visitors were aware of the role of the zoo in protecting endangered species.

Our second example is from China. Davey (2006b) investigated visitor interest, as measured by viewing times, at a mandrill *Mandrillus sphinx* enclosure at Beijing Zoo. He found that visitors spent more time at the enclosure after it had been transformed from a **barren enclosure** to a more naturalistic one, even if there was no animal visible. This is an encouraging result at a time when Beijing (and probably other Chinese zoos) is faced with the long task of replacing its old concrete enclosures with naturalistic ones. Davey (2006b) also found that Chinese people's perceptions of the role of zoos and animal welfare were generally positive, particularly in those that visited the zoo.

Finally, Puan and Zakaria (2007) undertook a questionnaire survey of visitors to three Malaysian zoos (National Zoo, Malacca, and Taiping) to find out how they perceived the role of zoos. Most of the respondents (80 per cent) were local, living in the same state as the zoo, and most visited with their families to see the animals. Encouragingly, the majority of respondents were well aware, and supportive, of the conservation role of zoos.

Figure 13.4 People enjoy seeing active animals. Felids, such as these snow leopards *Panthera uncia*, do not attract much attention when asleep (a), but become transformed when they are awake and active (b). (Photographs: Geoff Hosey)

that the animals were bored or sad) among the general public, attitudes among those actually in the zoo were more positive. With the trend towards naturalistic enclosures, we might hope that people's perceptions of zoos and their animals would become more positive, and this does, indeed, appear to be the case. Although visitors still spend very little time at the enclosures, they do rate naturalistic or enriched enclosures more favourably (Wolf and Tymitz 1981; Tofield *et al.* 2003). This appears to be because people assume that animals in naturalistic enclosures have the best welfare, and it has been suggested that visitors who see animals performing repetitive and abnormal behaviours perceive them to be 'unhappy' or 'bored' (McPhee and Carlstead 2010). Some support for this comes from a study by Miller (2012), who found that people who had viewed a video of a tiger pacing rated its welfare lower than people who had watched a video of a tiger resting. Conversely, Melfi *et al.* (2004b) found that the people they interviewed preferred to see tigers being active and thought that this would indicate good welfare, even though they accepted that this was not what tigers spent their time doing in the wild. So people may have contradictory notions about what best welfare actually is.

13.1.4 Do zoo initiatives change attitudes?

The more naturalistic enclosures that zoos have been providing in recent years ought to promote more positive views among zoo visitors about the welfare and naturalness of the animals (Coe 1985), and studies such as those described in the previous section suggest that this is, indeed, the case. But other changes that are made to the way in which the animals are maintained may also influence people's perceptions and therefore need to be monitored. The hope, of course, is that changes that are instigated to improve animal welfare will also be seen more positively by the zoo-going public, but this cannot be taken for granted.

McPhee *et al.* (1998) tested the effects of **environmental enrichment** on public attitudes by interviewing people in front of each of four exhibits: a barren outdoor polar bear *Ursus maritimus* grotto, a vegetated outdoor tiger grotto, a traditional barred outdoor lynx *Lynx* spp. cage, and an indoor **immersion exhibit** for a fishing cat *Prionailurus viverrinus*. Each enclosure also had a natural object (for example, wood), a non-natural object (for example, a blue plastic barrel), or no object present. They were testing a common assumption that the public see non-natural objects provided for **enrichment** purposes as artificial, and that this leads to more negative perceptions of the zoo and the animals. In fact, they found that the type of enrichment provided hardly influenced attitudes at all, regardless of enclosure type, and that visitors generally understood the function and importance of the enrichment objects. Similar results were found by Kutska (2009), who showed that the perceptions of naturalistic and non-naturalistic enrichments did not differ among visitors to the polar bear exhibit at Central Park Zoo, New York (see **Chapter 8** for more on enrichment).

On the other hand, a study at Beijing Zoo by Davey *et al.* (2005) found that visitor behaviour changed when viewing an enclosure in which enrichment had been added. In particular, viewing and stopping times increased in comparison with those at the enclosure prior to enrichment. The enrichment in this case included addition of more naturalistic items to a previously barren mandrill enclosure.

Similarly, Blaney and Wells (2004) found that the addition of camouflage netting to a gorilla *Gorilla gorilla* enclosure (put there to try to reduce the stressful effect of zoo visitors) improved the public's perception of the animals and their enclosure.

Not all kinds of enrichment are as readily acceptable to the public. In principle, if it is important for zoos to give their animals the opportunity to show **species-typical behaviours**, then zoo **carnivores** should be afforded the opportunity to hunt live prey—but how would the public view this? Ings *et al.* (1997a) attempted to find out by interviewing visitors to Edinburgh Zoo,

Type of feeding	On-exhibit	Off-exhibit	Reference
Live insects to lizards	96	100	Ings *et al.* 1997a
Live insects to lizards	87.3	82.6	Cottle *et al.* 2010
Live fish to penguins	72	84.5	Ings *et al.* 1997a
Live fish to otters	82.6	80	Cottle *et al.* 2010
Live rabbit to cheetah	32	62.5	Ings *et al.* 1997a
Live rabbit to tiger	48.4	68.2	Cottle *et al.* 2010

Table 13.1 Percentage of people at Edinburgh Zoo (Ings *et al.* 1997a) and Zurich Zoo (Cottle *et al.* 2010) who agreed with the idea of feeding live prey to zoo animals on-exhibit and off-exhibit

and more recently a similar, but questionnaire-based, survey has been conducted at Zurich Zoo (Cottle *et al.* 2010). The results of these studies (see **Table 13.1**) imply that the public—or at least those who go to zoos—may not be as opposed to this idea as we might expect, particularly if the feeding of live prey is done off-exhibit. At present, of course, it is not legal to do this with vertebrate prey in the UK (see **Chapter 12**).

13.2 Education and awareness raising

Educating the public about animals, and raising their awareness and support of conservation, are both a fundamental part of the modern zoo's mission, so we can justifiably ask how successfully zoos achieve this. In this context, 'education' can mean a sort of passive acquisition of knowledge that comes from seeing the animal and reading the notices (**Fig. 13.5**), and this is often referred to as **informal learning**. Increasingly, however, zoos are using more structured forms of instruction, ranging from keeper talks and demonstrations, through to school and college visits (**Fig. 13.6**) and short courses, all of which we can refer to as **formal learning**. Most zoos have tended to concentrate on the latter, and have rather neglected 'free-choice' learning (Moss and Esson 2013).

Education departments have now become widespread in zoos (Woollard 1998), and zoo educators undertake a variety of activities, including giving talks, volunteer training, and outreach

Figure 13.5 A good example of how zoos can provide information to their visitors and create passive learning experiences is through the provision of informative signs, which can be produced to interest visitors of all ages. (Photograph: Sheila Pankhurst)

work (Woollard 1999). Surveying all the educational activities and initiatives that zoos have introduced in the last couple of decades is outside the scope of this book, but we can briefly consider what impact these activities have, particularly on people's knowledge of, and attitudes towards, conservation.

13.2.1 Education as part of zoos' missions

Education is one of the four major purposes of modern zoos (see **section 2.5.1**), so it is not surprising that this figures prominently in their mission statements (Patrick *et al.* 2007). A survey by Mason (2008) at Wellington Zoo in New Zealand

Figure 13.6 Active learning in zoos can be achieved by providing informed guides to zoo visitors. In this case, information about animals at Apenheul Primate Park in the Netherlands was presented to a visiting group of university students by a trained guide. (Photograph: Sheila Pankhurst)

revealed that visitors do perceive this to be an important role of the zoo, but also think that entertainment is one of the zoo's major functions, and are much less aware of the conservation importance of zoos. One reason for this may be that zoo websites (which, after all, are probably a primary source of many visitors' information) tend to promote entertainment more than conservation, and describe their conservation work rather superficially (Carr and Cohen 2011). Although zoos may see clear connections between conservation, education, and entertainment, these may not always be obvious to those outside the zoo world (Fraser and Sickler 2009), so that leads us to ask how well zoos achieve their education mission. It is clearly important to do this, but surprisingly few zoos actually do, at least in the AZA realm (Luebke and Grajal 2011), mainly because of resource limitations, and it is likely that this is true elsewhere in the world as well. Nevertheless, a substantial amount of education evaluation has taken place

in zoos, so we now know much more about the effectiveness of different activities.

13.2.2 Formal learning at the zoo

Most zoos offer structured educational opportunities, both to ordinary visiting members of the public (such as keeper talks, close encounters, etc.), and to school and college students on organized visits (**Fig. 13.7**). They may also run courses and workshops for zoo and other professionals in topics such as animal welfare (Melfi and Hosey 2011) and conservation (Askue *et al*. 2009). Recently several zoos in collaboration with universities (see **section 14.3.5**) have also given zoo visitors the opportunity to view and engage with scientific research ('public engagement with science'), and several have attempted to evaluate the success of this (Bowler *et al*. 2012; Waller *et al*. 2012). In the UK and Ireland, 760,000 school pupils use the educational services of BIAZA member zoos each

Figure 13.7 School visits provide children with the opportunity to learn about the role of zoos and how they function, but also about the animals that they maintain, and a wider range of issues relating to nature and the environment. (Photograph: Sheila Pankhurst)

year, with 400,000 of these receiving some kind of formal tuition (figures from BIAZA).

School and college visits often include 'hands-on' sessions with live animals and animal parts (for example, fur and bones), and teachers rate these sessions as the most valuable part of the visit (Woollard 2001). It is widely thought that childhood experiences of zoos are important in fostering positive attitudes to the environment in adults (Holzer and Scott 1997), which would emphasize the value of school visits—but comparison of the content of conversations at London Zoo between, on the one hand, children on a school visit and, on the other, family groups showed no difference between the two, leading the authors to suggest that schools are failing to make full use of the educational potential of zoos (Tunnicliffe *et al.* 1997).

What about the less structured events, such as keeper talks (**Fig. 13.8**)? Given that visitors prefer to see active animals, then the time they spend

at an exhibit should be greater if there are animal presentations accompanied by keeper talks (see **section 13.1.2**). Does this also increase educational opportunities?

Broad (1996) used a questionnaire-based study at Jersey Zoo to evaluate the relative effectiveness of three different educational media (guidebook, signs, and keeper talks) in enhancing people's understanding of the zoo's conservation work and their knowledge of endangered species. She found that keeper talks were the most effective of the three, as we would probably expect. Given that a large proportion of the respondents had a high level of education, belonged to one of the higher socio-economic groups, and were visiting the zoo because they were interested in wildlife, it is not clear how applicable these results are to other zoos and other countries.

A similar study at Point Defiance Zoo in Tacoma compared visitors watching clouded

Figure 13.8 Keeper talks can include opportunities for the public to meet and question the keepers (a), while handling sessions with some of the animals (b), which can bring them 'up close and personal' with animals, and demonstrations of what the animals are able to do (c) can all leaving lasting impressions on the zoo visitor. These methods contribute to educating visitors and providing them with a lasting memory of their visit (see **section 6.1.3**). (Photographs: (a) Vicky Melfi; (b) South Lakes Wild Animal Park; (c) Geoff Hosey)

leopards *Neofelis nebulosa* in a traditional exhibit and in an interpretive presentation, which consisted of encountering a keeper walking the leopard around the zoo and answering visitors' questions (Povey and Rios 2002). Visitors meeting the interpretive presentation spent longer watching the animal and sought more knowledge than those seeing only the traditional exhibit. Similarly, school students visiting Potter Park Zoo in Lansing, Michigan, retained more information after an interpretive session than when a more factual presentation was given (Visscher *et al.* 2009). We should bear in mind that the use of animals in interpretive displays opens up a realm of ethical and potentially welfare issues. Similarly, at Zoo Atlanta visitors appeared to learn more from video or live keeper presentations than just from signs (Perdue *et al.* 2012) (**Fig. 13.9**).

13.2.3 Do zoos raise conservation knowledge and awareness?

Zoos have an important role to play in educating the public about animals and nature in general, but their role in conservation education is particularly important. The term 'conservation education' refers to '*the principles of environmental education and education for sustainability*' (WAZA 2005).

Zoos are uniquely well placed to undertake effective conservation education (Whitehead 1995; Sterling *et al.* 2007) by capitalizing on their live animal collections, and the *in situ* and *ex situ* work with which they are involved. This involves raising awareness of conservation issues, but also demonstrating the links between the animals in the collection and the conservation of their wild counterparts (**Fig. 13.10**), so that the zoos effectively become interactive and entertaining

Figure 13.9 Signage in zoos, represented here by the Bronx Zoo in (b) New York, (a, d), Toronto Zoo, and (c) Nagoya Primate Zoo, Japan, is highly variable, both in terms of the information that is being conveyed and also in the manner in which it is depicted. These are some examples that illustrate signs designed to inform visitors about the basic natural history of the animals and the way in which they are managed in the zoo. (Photographs: Vicky Melfi)

conservation centres (Tribe and Booth 2003). But how effectively do zoos achieve this?

To some extent, we might expect that the mere act of visiting a zoo, and encountering the animals and information about them, would help to make visitors more conservation-oriented, and this seems to be, at least partly, the case. At the National Aquarium in Baltimore, USA, for example, the conservation knowledge, attitudes, and behaviour of visitors were measured on arrival at
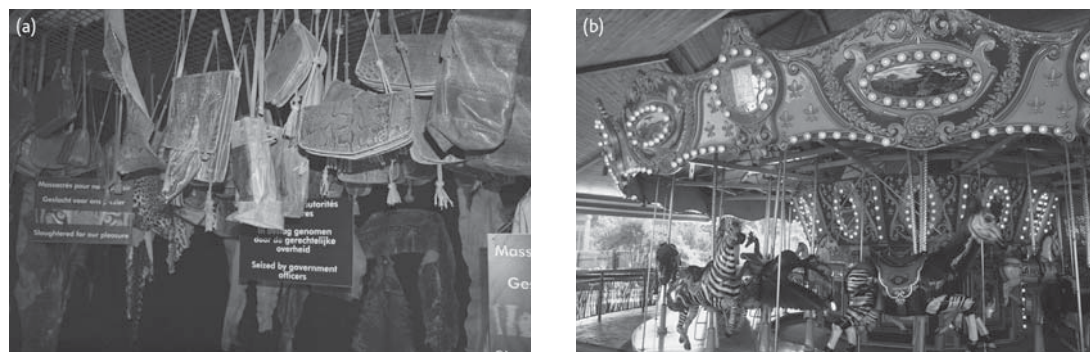
Figure 13.10 Conservation education often involves demonstrating the links between the zoo and *in situ* conservation, as in (a) this display of the effects of illegal trafficking of animal parts, or may just raise awareness through entertainment, as in (b) this conservation carousel at Dallas Zoo (Photographs: Jeroen Stevens)

the aquarium, again at departure, and then again 6–8 weeks later (Adelman *et al.* 2000). The results of the study indicated that a raised knowledge and understanding of conservation persisted in people after their visit to the aquarium, but did not result in them initiating any conservation-related actions. At the Bronx Zoo, a new 'Congo Gorilla Rainforest' exhibit, which visitors had to pay extra to visit, included not only the simulated African rainforest with over 300 animals, but also an exhibition building with interpretative and interactive panels and displays. Extensive monitoring and questioning of visitors revealed an increase in their knowledge and concern about conservation after touring the exhibit (Hayward and Rothenberg 2004).

Other studies have reported slightly different results. A survey of attitudes and knowledge amongst zoo visitors entering and leaving several UK zoos found no differences between these two groups in any of the measures used except one: on leaving, visitors had more idea about what differences they could make to conservation (Balmford *et al.* 2007). This result is consistent with the suggestion that education through facts about conservation is not enough in itself; people want to know what they can do personally (Gwynne 2007; Sterling *et al.* 2007).

A number of other techniques have been used to try to enhance the environmental knowledge and awareness of the zoo-visiting public. For example, at Zoo Atlanta, Georgia, an exhibit about the bushmeat crisis, consisting of photographs and accompanying text of live animals, dead animals, logged areas, and hunting pictures, was installed in the Willie B. Conservation Centre.[6] Although the pictures of dead animals were disturbing, 97 per cent of visitors who were asked about them thought that it was appropriate for the zoo to show them to adult visitors. Eighty-three per cent of the visitors had not heard of the bushmeat trade, so the exhibition did raise awareness, but visitors' conservation-related knowledge was not increased by the exhibition (Stoinski *et al.* 2002).

Improving knowledge and awareness is one thing; bringing about a change in behaviour is, of course, something entirely different. It is also very difficult to measure, because people might not recognize small changes in their behaviour as a result of zoo education to be anything to do with conservation at all. Studies at Monterey Bay Aquarium, California, showed that conservation education was most successful if courses of action were suggested to visitors that they were actually able to take, as mentioned above, and which were still consistent with their lifestyle. For example, at the aquarium visitors could pick up a 'Seafood Watch' pocket guide, which listed sustainable seafood to buy in restaurants and shops, and also an 'Ocean Allies Card', which listed conservation organizations that they could join. Visitors turned out to be more interested in changing their eating habits than in joining a conservation organization (Yalowitz 2004).

The educational impact of zoos has been investigated by an AZA three-year project (Falk *et al.* 2007), during which the authors surveyed the literature, held public forums with a selection of AZA institutions, and interviewed zoo visitors. The study showed that visits to zoos and aquariums do, indeed, raise awareness and a sense of connection to nature, as well as promoting knowledge about, and caring for, conservation. However, it was also the case that visitors came with more ecological knowledge than expected, so the zoos were supporting and reinforcing the existing values and attitudes of the visitors[7]. But, ultimately, we probably need to recognize that people come to the zoo primarily for a good family day out and to see some animals rather than to be educated, even if, when asked, they think that zoos ought to be educating people about conservation (Reading and Miller 2007). The challenge is to deliver the conservation message within that enjoyable experience.

Finally, we can note that most educational initiatives that zoos put on are aimed at children or at

---

[6] Willie B. was a famous gorilla who lived at what is now Zoo Atlanta, Georgia, for nearly 40 years (see **Box 2.3**).

[7] We should perhaps point out that there has been an ongoing debate about the validity of the methods used in this study, and if you like a bit of an argument you can read it at Marino *et al.* (2010) and Falk (2010).

general zoo visitors. However, these might not be the most appropriate target. Conway (2007), for example, has urged that more should be done to target policy-makers, with a view to influencing their attitudes and actions. As Conway points out: '*Today's children will not be decision-makers until billions more children have been born and much more wildlife has been lost*'.

13.3 Humans in the zoo: how do they affect the animals?

It is time now to turn our attention away from the zoo visitors themselves and to consider what the presence of people means to the animals in the zoo. As we have already pointed out, humans are a significant part of the environment in which zoo animals live; those humans may be daily visitors, or they may be people who work in the zoo and therefore, to differing degrees, become familiar to the animals. It is reasonable for us to ask if, and how, the animals are affected by these people.

13.3.1 Zoo visitors

One of the first people to try to identify how animals in zoos might perceive the humans with whom they came into contact was Heini Hediger,[8] whose evidence was anecdotal, but which nevertheless helped lay the foundations of modern zoo biology. Hediger (1965) considered that humans could be significant to animals in five different ways:

- as an enemy (that is, to be avoided);
- as prey;
- as a symbiont (that is, as a partner working towards a common goal);
- as of no consequence (that is, part of the background to be ignored);
- as a **conspecific** (for example, a rival or a sexual partner, both of which would cause problems).

Clearly, the particular way in which an animal views people will depend upon its species, its prior experience of human interaction, and the people involved (and probably other variables as well). Of all of these factors, the one that probably impacts most on the welfare of the animals is when they perceive humans as enemies, but systematic studies are necessary to find out if they do view us this way (Hosey 2013).

Do human visitors affect zoo animals at all?

The first question to ask is whether human zoo visitors really do affect the behaviour of the animals (**Fig. 13.11**). It is, after all, possible that the animals perceive visitors as being (in Hediger's words) 'of no consequence'. However, many studies have shown that there is an association between visitor numbers and activity, and changes in behaviour of animals. For example, one of the earliest studies showed that zoo primates were more active, changed their dispersion in the cage, and displayed more visitor-directed behaviour at large active groups of humans than they did at small non-active ones (Hosey and Druck 1987). Mitchell *et al.* (1992b) pointed out that these results could, however, be explained in terms of more active animals attracting bigger and more interactive crowds of visitors.

Hosey (2000) has consequently referred to the 'visitor effect hypothesis' and 'visitor attraction hypothesis' as two alternative explanations of the relationship between zoo animals and their audiences; much of the evidence for zoo primates is consistent with the 'visitor effect hypothesis' (see below), but there is also evidence for the 'visitor attraction hypothesis'. Margulis *et al.* (2003) showed that small cats attracted more visitors when they were active, but the cats were generally unaffected by human audiences. As this paper points out, the two phenomena probably have some mutual effect and are not independent of each other.

---

[8] Heini Hediger (1908–1992) was, for a long time, Director of Zurich Zoo and collected years of observations on the lives of animals in zoos. He can be regarded as one of the founders of modern zoo biology.

Figure 13.11 Zoo visitors behave towards captive animals in all sorts of different ways, ranging from (a) climbing the railings and trying to attract the animal's attention, and (b) teasing the animals, in this case with a pet dog, to (c) passively standing or sitting and watching the animals. (Photographs: (a) Sheila Pankhurst; (b and c) Geoff Hosey)

Negative effects of zoo audiences on animals

If zoo visitors do affect the behaviour of the animals, then, clearly, we need to know the nature of that effect. Human visitors are a significant component of the zoo environment, and zoos are only really able to fulfil their missions and achieve their aims by attracting more visitors. If those visitors change the behaviour of the animals, then we need to know how.

Most of the studies of zoo visitor effects have been done on primates and the evidence overwhelmingly points to the conclusion that the effect is generally negative—that is, that the presence of zoo visitors results in the animals displaying behaviours that are usually associated with a stress **response**. Because of this, there is a risk that prolonged exposure to human visitors could adversely affect the welfare of the animals.

Much of this literature has been reviewed by Hosey (2000; 2013). An early study by Chamove *et al.* (1988) at Edinburgh Zoo showed that **agonistic behaviour** increased and affiliative behaviour decreased in three different primate species (Diana monkey *Cercopithecus diana*, cotton-top tamarin *Saguinus oedipus*, and ring-tailed lemur *Lemur catta*) when human audiences were present (**Fig. 13.12**). Similar results were reported at Rotterdam Zoo by Glatston *et al.* (1984) in relation to cotton-top tamarins housed on-show, compared with those housed off-show, and by Mitchell *et al.* (1991a) in relation to golden-bellied mangabeys *Cercocebus galeritus chrysogaster* at Sacramento Zoo, USA. In this study, animals were moved between enclosures that attracted high or low visitor attendance because of their location in the zoo, and the animals changed their behaviours accordingly.

More recent studies have shown broadly similar effects. For example, gorillas *Gorilla gorilla* at Belfast Zoo show more intraspecific aggression and abnormal behaviours on summer weekends when visitor numbers are high than during the winter, when visitor numbers are low (Wells 2005), orang-utans *Pongo* spp. at Chester Zoo are affected by noisy visitors in particular and try to cover their heads with paper sacks (Birke 2002), and lion-tailed macaques *Macaca silenus* in Indian zoos show up to 20 per cent more abnormal behaviour when confronted with zoo visitors (Mallapur *et al.* 2005).

All of these studies infer, from behavioural data, that the animals are being stressed by the presence of human visitors. These behavioural indicators of stress include increased abnormal behaviours,
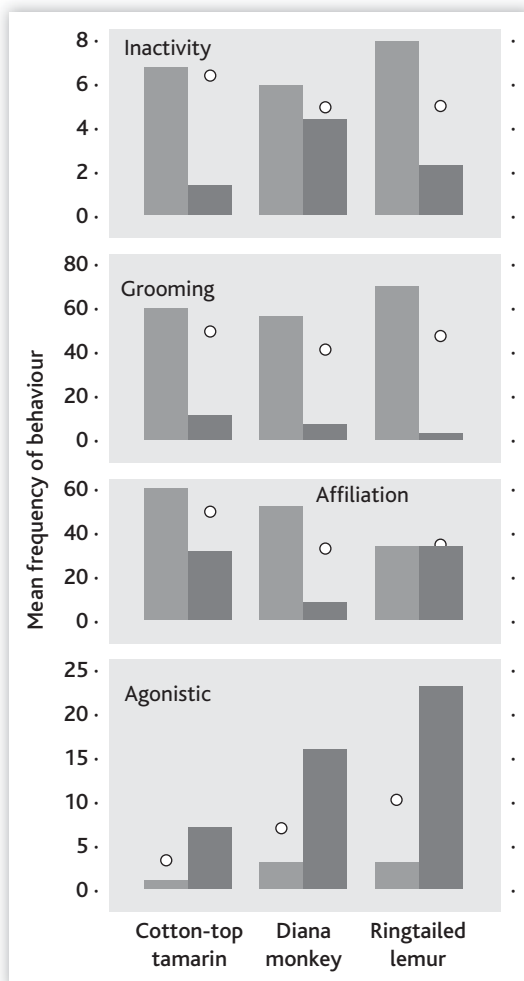
Figure 13.12 This shows the frequency (taken at 10 second intervals) of four different behaviours of three primate species at Edinburgh Zoo. The pale bars indicate when there were no human visitors present, the dark bars show when people were present, and the circles show the animals' behaviours when the visitors crouched down so that only their heads were visible to the animals. When the visitors crouched, the change in the animals' behaviour (compared with when no visitors were present) was less pronounced. (From Chamove *et al.* 1988)

particularly **stereotypies** (see **Chapters 4** and **7**), increased intra-specific (that is, between cage-mates) and inter-specific (that is, towards humans) aggression, increased activity (sometimes measured as decreased inactivity),[9] and, sometimes,

---

[9] Activity and inactivity are not necessarily the reciprocals of each other, because each may or may not include certain other behaviours.

---

decreased affiliative behaviours, such as grooming. However, a comparison across studies does indicate some variability and inconsistency in the behavioural responses of different primate groups to zoo visitors. Even within the same species, different individual animals may respond differently to humans (Hosey 2008; Kuhar 2008). This is probably because the way in which different animals change their behaviours in response to stressors is itself affected by a number of other variables, such as cage space and complexity, species, and visitor behaviour. For example, Wood (1998), found a quite complex interrelationship between the responses of chimpanzees *Pan troglodytes* at Los Angeles Zoo to human audiences, the sizes of audience groups, and whether or not the environmental enrichment supplied to the animals was new. It is also likely that the previous history of interactions that animals have had with people affects how they subsequently respond (Hosey 2008).

Of course, inferring stress from behaviour is something that should be done with caution (see **Chapter 7**). An alternative approach is to use physiological measures, which perhaps provide a more direct measure of the animal's welfare, although here again demonstration of a change in the amount of the measured variable does not necessarily mean that there is a welfare issue. Davis *et al.* (2005) found a correlation between visitor numbers and urinary cortisol levels in Colombian spider monkeys *Ateles geoffroyii rufiventris* at Chester Zoo (see **Box 7.3**). Faeces are another source of cortisol, and in black-buck *Antelope cervicapra* at Arignar Anna Zoo in Chennai, India, levels of faecal cortisol are higher when there are more people in the zoo (Rajagopal *et al.* 2011). Finally, cortisol can also be obtained from saliva, and Montanha *et al.* (2009) were able to demonstrate higher levels of salivary cortisol in jaguars *Panthera onca* at Brasilia Zoo than at a conservation breeding centre which had low levels of public attendance (**Fig. 13.13**).

Can stressful effects of human audiences be reduced?

If human visitors are stressful to zoo animals, then we can reasonably ask if there are ways of reducing
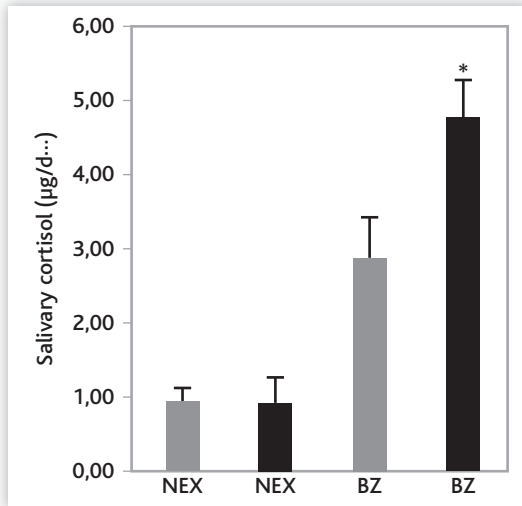
Figure 13.13 Levels of salivary cortisol in jaguars at Brasilia Zoo and at a conservation breeding centre, on no-visitation (pale bars) and high-visitation (dark bars) days. Although the cortisol levels are significantly lower in the breeding centre jaguars, they did not increase on high-visitation days, suggesting that enclosure characteristics, as well as visitor numbers, may contribute to the animals' response (adapted from Montanha *et al.* 2009).

Figure 13.14 It is not uncommon for zoos to use measures in an attempt to reduce the visitor pressure on some of their captive animals. In this case, a camouflage barrier has been erected outside an enclosure at Edinburgh Zoo, to try to make the presence of human visitors less obtrusive to the animals. (Photograph: Sheila Pankhurst)

their stressful effect. In the study by Chamove *et al.* (1988) referred to above, visitors were asked to crouch, rather than stand, at the viewing windows of the three primate enclosures, on the grounds that the animals might perceive them as less of a threat. This did, indeed, have the effect of reducing the impact of the visitors on the animals' behaviour, although the behaviours of the primates were still different to their behaviours when no visitors at all were present. The suggestion from this was that enclosures could be designed with lowered public walkways, to achieve a similar effect.

Existing enclosures can be modified by the addition of screening (**Fig. 13.14**), or additional places (refuges) for the animals to hide from view. A camouflage net barrier was added to the gorilla enclosure at Belfast Zoo by Blaney and Wells (2004) to reduce the visual impact of the human visitors. It resulted in less conspecific-directed aggression and stereotyped behaviour by the gorillas than when the barrier was absent; furthermore, the barrier was rated positively by members of the public, who considered it made

the gorillas look more exciting and less aggressive. A similar study by Keane and Marples (2003) at Dublin Zoo, again looking at gorillas, found that a barrier was more effective in reducing the stress behaviours of the animals than the use of carpets in the public walkway (to reduce noise) and signs asking visitors to be quiet.

The use of signs to modify visitor behaviour has not been evaluated to any great extent (**Fig. 13.15**), but has been tried in an aquarium setting by Kratochvil and Schwammer (1997). They attempted to reduce the amount of banging on the glass fronts of aquarium tanks by the public at Tiergarten Schönbrunn in Vienna. Such knocking sets up high sound pressure levels, and leads to startle responses and avoidance in fish. To try to reduce it, they tried out three different signs saying:

1. 'Knocking kills fish'
2. 'Only loonies would knock'
3. 'Please don't knock on the glass'.

The second of these signs had the greatest success (**Fig. 13.16**), reducing knocking to less than 10 per cent of baseline; the third had the least effect.

A more active way of reducing the stressful effects of human visitors might be to improve
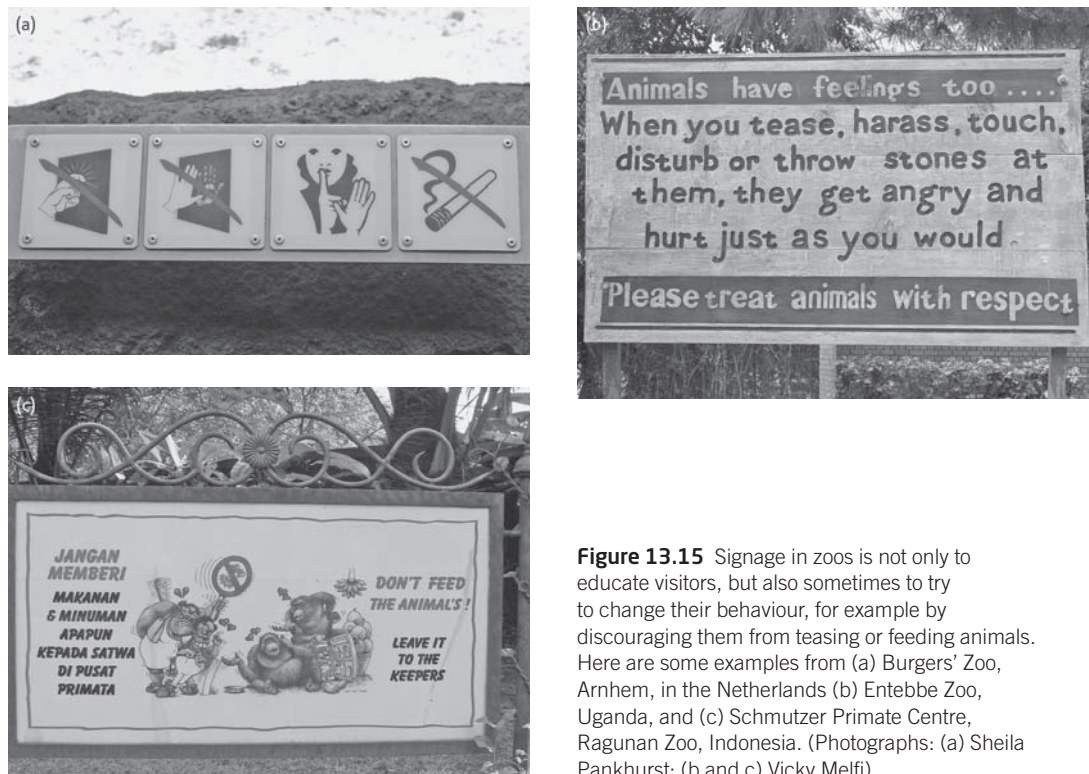
Figure 13.15 Signage in zoos is not only to educate visitors, but also sometimes to try to change their behaviour, for example by discouraging them from teasing or feeding animals. Here are some examples from (a) Burgers' Zoo, Arnhem, in the Netherlands (b) Entebbe Zoo, Uganda, and (c) Schmutzer Primate Centre, Ragunan Zoo, Indonesia. (Photographs: (a) Sheila Pankhurst; (b and c) Vicky Melfi)

the animals' perceptions of people by fostering positive relationships with them. So how can this be achieved?

One way might be through **positive reinforcement training** (see **section 13.4.1** for more on this). In a study at Paignton Zoo Environmental Park, interactions between Abyssinian colobus monkeys *Colobus guereza* and zoo visitors declined significantly after the monkeys were trained to undergo oral examinations (Melfi and Thomas 2005).

Can zoo visitors be enriching?

If animals in zoos really are stressed by the presence of people, then clearly this could lead to
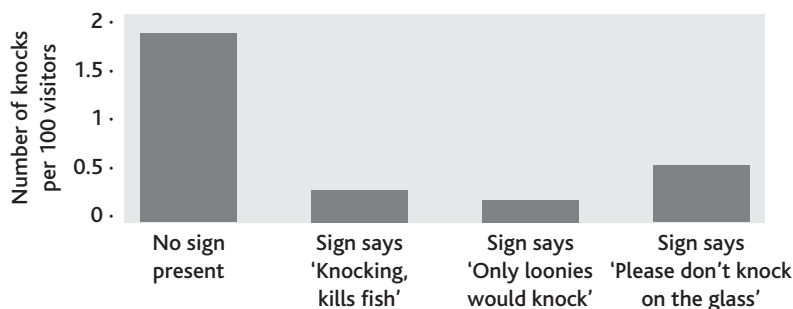
Figure 13.16 Signs at the aquarium in Schönbrunn Zoo in Vienna were effective in reducing the amount of knocking on the glass by zoo visitors. However, simply asking people not to knock was not as effective as implying that they would be 'loonies' if they did. (Adapted from Kratochvil and Schwammer 1997)

conflict between animal welfare and the educa-
tion, conservation, research, and entertainment
roles of the zoo (Fernandez *et al.* 2009), so it
would be worthwhile to try to find ways of mak-
ing encounters between animals and people less
stressful and more enriching. The suggestion that
zoo visitors might be enriching to zoo animals was
probably first made by Desmond Morris (1964),
who considered that zoo animals were bored for
much of the time and that human visitors might be
a welcome source of variability in what was other-
wise a monotonous environment. Unfortunately,
evidence in favour of this suggestion is sparse. A
study of green monkeys *Cercopithecus aethiops
sabaeus* at Mexico City Zoo (Fa 1989) failed to
find any increase in agonistic behaviour on days
when the public had access compared with days
when the zoo was closed. Instead, the monkeys
spent much time and effort attempting to get
food from the visitors, which, from their point of
view, might have meant that they were enriched
rather than stressed. Similarly, chimpanzees *Pan
troglodytes* at Chester Zoo are willing to engage
in quite long interaction sequences with human
visitors, apparently in the hope of being thrown
food (Cook and Hosey 1995). Finally, orang-utans
Pongo pygmaeus in a free-ranging tree-top exhibit
at Singapore Zoo showed no stress-related behav-
iours in response to visitor presence, but did start
begging when visitor numbers reached about forty
at the exhibit (Choo *et al.* 2011).

Some of the enrichment attempts initiated by
Hal Markowitz in the 1970s, which involved the
use of operant techniques to shape the animals'
behaviours, could also involve zoo visitors. An
example is the apparatus set up for gibbons at
Portland Zoo, in which visitors could insert a coin
into a machine, thus turning on a light that sig-
nalled to the gibbons that a lever press would bring
about a food reward at the other side of the cage
(Markowitz and Woodworth 1978). This raised
both activity levels of the gibbons and revenue for
the zoo, and might be regarded as a more positive
response by the animals to human visitors.

But to what extent can we regard the presence
of human visitors as enriching in these studies?

Fa (1989) has suggested that feeding by the pub-
lic can result in overfeeding, with long-term ad-
verse consequences for health and reproduction.
He also points out that the food-directed behav-
iours of the monkeys in his study were done at
the expense of other behaviours, such as social
behaviour. Similarly, the sorts of techniques used
by Markowitz, generally referred to as **behav-
ioural engineering**, have been criticized on the
grounds that they promote 'artificial', rather than
'naturalistic', behaviours (Hutchins *et al.* 1978).
Whether or not these changes in behaviour are
the result of enrichment probably depends on
how you measure enrichment (see **Chapter 8**).
Other circumstances in which audiences might
be enriching for zoo animals might be through
increased opportunities for inter-specific interac-
tion (see Claxton (2011) and later in this section)
(**Plate 13.1**). Thus, bottlenose dolphins *Tursiops
truncatus* across a number of aquariums showed
higher rates of behavioural diversity, diversity of
swimming styles, and play behaviour after taking
part in shows and interaction events, implying
that the opportunity to take part in these shows
was enriching for the animals (Miller *et al.* 2011b)
(**Fig. 13.17**). There was also evidence that such
shows increased conservation-related knowledge
and attitudes in visitors to the shows (Miller
et al. 2013). Interactive shows are now a feature of
many zoos (see **Chapter 15**), but in general their
consequences for the welfare of the animals has
not been investigated.

Zoo visitors as of no consequence

We started this section on zoo visitors by noting
Hediger's (1965) suggestions of how people may
be perceived by animals. One of his categories was
that animals might consider people to be of no
consequence: just part of the background to be ig-
nored. Is there any evidence to support this view?

Until recently, it was quite a widely held view
that zoo animals **habituate** to members of the
public—that is, that they get used to them and
no longer respond to their presence—but there
is actually very little data for us to be able to say
whether or not this is true. As we have seen above,
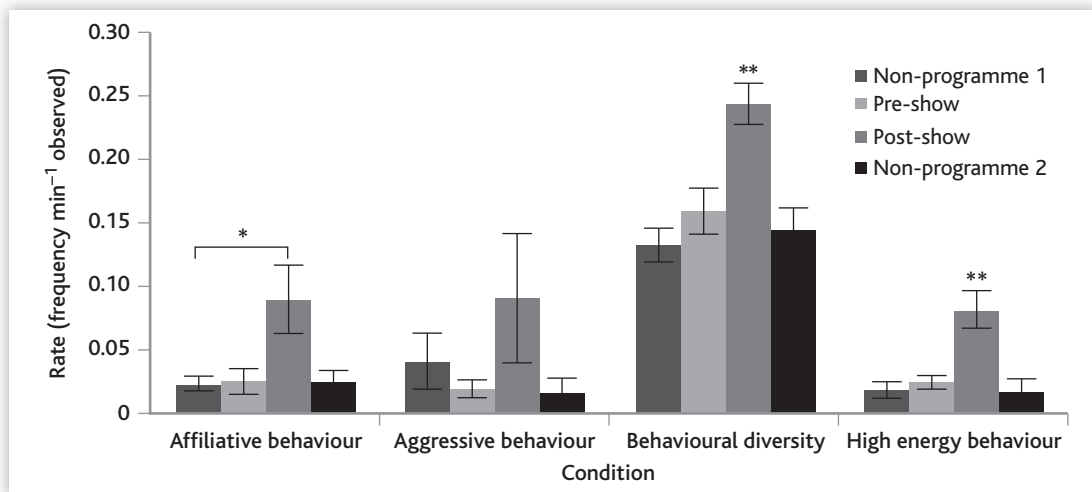
Figure 13.17 After taking part in an interactive show, bottlenose dolphins *Tursiops truncatus* showed increases in affiliative behaviours and behavioural diversity. Asterisks denote the presence of significant differences between conditions. (Adapted from Miller *et al.* 2011b)

primates do not usually ignore zoo visitors. What about other kinds of animal?

A study at Fota Wildlife Park, Ireland, by O'Donovan *et al.* (1993) failed to find any significant changes in the behaviour of a group of cheetah *Acinonyx jubatus* in response to the presence of zoo visitors. More recently, Margulis *et al.* (2003) scored the behaviours of six species of felid in seven different enclosures at Brookfield Zoo, Chicago, during both spring and summer periods. They found no significant effects of visitor presence on any behaviours of the cats, although, as we noted previously, they also found that, when the cats were active, they attracted more interest from the visitors. Other studies on felids seem to agree that these animals do not respond to zoo visitors in the way that many primates do (**Fig. 13.18**), although there may be visitor-related changes in stereotypy (Mallapur and Chelan 2002; Sellinger and Ha 2005).

Why should felids fail to respond to zoo visitors while primates show such a clear and obvious response? Margulis *et al.* (2003) suggest simply that some animals are more reactive than others and that this may be **taxon**-specific. In addition, of course, zoo visitors are themselves primates, and share many communicative signals with monkeys and apes. But there is increasing evidence that, even

Figure 13.18 The assumption that all animals are negatively affected by zoo visitors seems unfounded. Felids, such as these lions *Panthera leo* at Paignton Zoo Environmental Park, do not seem to respond aversively towards zoo visitors as many primates do. (Photograph: Paignton Zoo Environmental Park)

after taxon differences have been taken into consideration, there are still individual differences in the way in which zoo animals respond to humans, and we will return to this in **section 13.3.4**.

Inter-specific communication

In the cases we have looked at so far, an effect of human visitors on zoo animals, and vice versa, has been inferred on the basis that the behaviour of one party has been changed by the presence and behaviour of the other, but we have not really examined the form that inter-species communication can take. Few studies have looked at the signals themselves, even though this can potentially give us a fascinating insight into the extent to which animals can discriminate and classify people.

A good example is the study by Mitchell *et al.* (1992a) on the golden-bellied mangabeys at Sacramento Zoo. They found that human visitors did numerous things that resulted in the monkeys threatening them, such as climbing the railings, leaning over, yelling, throwing ice from soft drinks, jumping up and down, making faces, and so on. These behaviours, collectively termed 'harassment', were performed more by boys and men than by girls and women; furthermore, the boys and men directed their harassment more at the male than the female mangabeys. In return, the male monkeys threatened the audience more than the females did and directed most of their threats to the male members of the audience. (Hediger's categories of how animals may perceive humans seem to work in the reverse direction as well.)

Another primate study is that of Cook and Hosey (1995), which looked at the exchange of signals between zoo chimpanzees and human visitors at Chester Zoo. Here again, male visitors tended to direct their behaviours at male chimpanzees, but harassment was less evident and much of what the chimpanzees did was best explained as soliciting food. Several chains of behaviour (interaction sequences) were seen and, in general, it was the human visitors whose behaviour was influenced by the preceding chimpanzee behaviour, rather than the other way around.

We might expect such interchanges between human and non-human primates more than between humans and other animal taxa, because of the similarity in morphology and signal form. For example, sheep and goats in a **petting zoo**

may show aggression or avoidance of humans (Anderson *et al.* 2002), which is consistent with the possibility that they perceive humans as potential predators or danger rather than as rival conspecifics, which seems to be the case with the mangabeys.

13.3.2 Human disturbance

Of course, not all the unfamiliar humans at the zoo are visitors who spend time looking at the animals. Others who come to carry out building, maintenance, or delivery work are probably more noticed by the animals as a result of the disturbance that they cause than because of their presence at the cage.

Again, it is remarkable how little the effects of this disturbance on the animals have been studied (**Fig. 13.19**). One study investigated changes in the behaviour of snow leopards *Uncia uncia* at Basel Zoo, Switzerland, during a period when the carnivore house next door was being demolished and rebuilt (Sulser *et al.* 2008). The cats responded to the noise by spending more time resting and by withdrawing to more remote parts of their exhibit. Both behaviour and cortisol excretion were monitored in two giant pandas *Ailuropoda melanoleuca* at the Smithsonian National Zoological Park in Washington, DC, while an adjacent cage was being demolished (Powell *et al.* 2006). The

Figure 13.19 Construction work often occurs over long periods in a zoo, as in this new lion house at Antwerp Zoo, but the effects of this on the animals living in nearby enclosures are not very well known. (Photograph: Geoff Hosey)

behaviours shown by both animals were characterized by the researchers as 'restless', and cortisol excretion increased although this may not have been related to the building work, because the fluctuations in secretion were different in the two animals.

A similar study at Honolulu Zoo, Hawaii, measured changes in behaviour and faecal corticoids in two species of Hawaiian honeycreepers (the 'Apapane *Himatione sanguinea* and the 'Amakihi *Hemignathus virens*) during ordinary days when routine maintenance work might or might not happen (Shepherdson *et al.* 2004). During the study, various disturbances occurred, such as evening concerts, people entering the cage to do maintenance work, people working on the roof, and machine noise. Faecal corticoid levels of the birds increased significantly when concerts or machine noise occurred compared with those on days on which nothing much happened, and these disturbances were also associated with behavioural changes, such as a reduction in foraging and perch hopping or flying.

13.3.3 Longer-term effects of visitors

All the studies we have looked at have been concerned with more or less immediate changes in the animals' behaviour and physiology when they are confronted with people or human disturbance. But there is also the possibility that in the longer term these responses could lead to other consequences for the biology of the animals. For example, there is evidence that laboratory chimpanzees change the timing of their births in order to give birth when there are the least number of people about (the 'weekend effect') (Alford *et al.* 1992). While this doesn't appear to occur in zoos (Wagner and Ross 2008), it does suggest that there may be subtle effects of human presence which we are not yet aware of. Some of these effects may have drastic consequences. The survival of Persian fallow deer *Dama mesopotamica* reintroduced to the wild was greatly influenced by whether they came from a zoo with high or low visitor numbers. Both sets of animals started to acquire predator-avoidance

behaviours after release, but less so in those which came from the zoo with high visitor numbers, with the result that none of these animals survived after 200 days, whereas 80 per cent of the animals from the zoo with low visitor numbers survived (Zidon *et al.* 2009). Clearly, we need to be concerned with more than just the immediate welfare of animals on public view.

13.3.4 Keepers

Keepers are probably perceived by animals in quite a different way from the visiting public; because of their longer and more intimate contact with particular animals, keepers or caretakers can develop more permanent relationships with the animals (**Fig. 13.20**).

Figure 13.20 Keepers have longer and more intimate contact with their animals than is possible for members of the public, so more permanent relationships can be established between keepers and individual animals. (Photograph: Julian Chapman)

All that is meant by 'relationship' in this context is that the two individuals have a history of interactions between them that lead to a greater predictability about the outcome of future interactions; in other words, they get to know what each other is likely to do. Such relationships can vary in quality, but the most positive kinds of relationship often lead to the formation of a 'bond' or 'attachment' between animal and human (Estep and Hetts 1992). The main characteristics of such a human–animal bond have been suggested (Russow 2002) as the involvement of a relationship between a human and an individual animal that it is reciprocal and persistent, and that it promotes an increase in well-being for both parties. Relationships can, of course, be of poor quality as well; the quality of interactions and, ultimately, of relationships between animals and their caretakers is an essential component of stockpersonship (often just **stockmanship**)—that is, the skill of managing and caring for animals.

Can animals discriminate between individual people?

For anecdotal evidence of whether animals can discriminate between individual people, you need only speak to a pet owner, farmer, zookeeper, or scientist, or indeed anyone who has worked or lived with animals for any length of time. Experimental evidence is harder to find.

In laboratory studies, using techniques such as **preference testing**, **operant conditioning**, and habituation, Davis (2002) has demonstrated discrimination between individual humans in rats, chickens, llamas, rabbits, sheep, cows, seals, emu, rhea, penguins, and honeybees. The literature on farm animals contains numerous studies that show discrimination of different people by the animals, often based on previous experience of being handled (e.g. de Passillé *et al.* 1996; Boivin *et al.* 1998). There is even some evidence from other species, including some reptiles (Bowers and Burghardt 1992) and the octopus (Mather 1992).

In any case, the results of studies on the human–animal relationship imply that animal discrimination of individual people is widespread.

Consequences of human–animal relationships

Once again, surprisingly few studies have been undertaken on human–animal relationships in the zoo. However, there is a lot of evidence from agricultural research that stockpeople differ in the way they interact with farm animals, leading to stockperson–human relationships (**Fig. 13.21**) of variable quality. The quality of these relationships has consequences for both animal production and animal welfare.

Much of the relevant literature is reviewed by Hemsworth (2003) and by Boivin *et al.* (2003). This research, which has particularly been done with cattle, pigs, and chickens, shows that some stockpeople have good relationships with their animals, the result of positive interactions with them, such as patting, stroking, and talking to the animals, and generally doing things rather
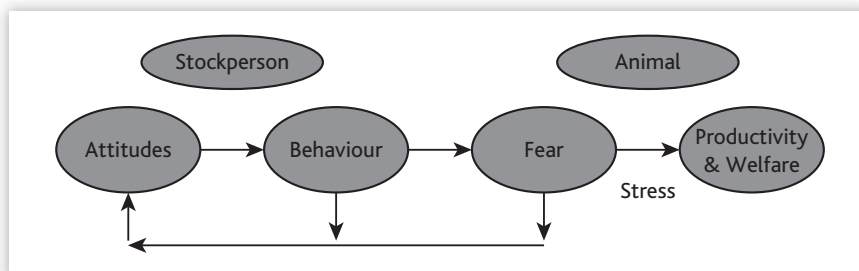
Figure 13.21 Hemsworth's model of human–animal interactions in agricultural animals is illustrated here. The stockperson's attitudes towards the animals affect the way in which he/she behaves towards the animals and this, in turn, can increase or decrease the fear that the animals have of people. This fear itself feeds back to affect the stockperson's attitudes and affects the productivity of the animals. (From Hemsworth 2003)

slowly. On the other hand, negative interactions such as slaps, hits, shouting at the animal, and fast movement lead to increased fear of humans in the animals. The resulting stress adversely affects the animal's welfare and can lead to a decline in productivity (for example, milk yield).

Among the most powerful predictors of the quality of stockperson–animal relationships are the person's attitudes and personality traits; the fearful response of animals to their interactions feeds back to and reinforce the stockperson's attitudes.

More recently, the importance of understanding human–animal interactions has been increasingly recognized among animal experimenters as well. Here, of course, part of that importance comes from a concern that a human–animal relationship can be a variable that is not unaccounted for (a **confounding variable**—see **section 14.4.2**) in experimental results, but evidence shows that relationships between experimenters and their animals can have beneficial, as well as aversive, effects (for example, see Dewsbury (1992) on laboratory rats).

In fact, the evidence from laboratory animals is very similar to that from farm animals. For example, in a study of laboratory stump-tailed macaques *Macaca arctoides* Waitt *et al.* (2002) found that the quality of the caretaker–animal relationship had an influence on the behaviour of the animals; those macaques that were considered friendly by their caretakers received more positive interactions from their caretakers during routine laboratory procedures (**Fig. 13.22**), and consequently were less disturbed by those procedures, and more likely to approach and accept food from their caretaker. Similarly, when caretakers spent more time with chimpanzees in a primate centre, the animals showed more grooming of each other and fewer abnormal behaviours, and interactions with the observer moved from 'mostly aggressive' to 'mostly friendly' (Baker 2004). Those who work with primates in laboratories are now very aware of the benefits of developing good relationships with their animals, while acknowledging that this also carries a down side, such as, for example, when the animal has to be euthanased (Coleman 2011).

Figure 13.22 Laboratory stump-tailed macaques *Macaca arctoides* that receive positive interactions from their keepers are less disturbed by routine laboratory procedures and more friendly with their caretakers. (Photograph: Keith Morris)

Keeper-animal relationships in the zoo

We would expect that what is true of farm and laboratory animals is also true of zoo animals and, from the very limited amount of research that has been done, this does, indeed, appear to be the case. Golden-bellied mangabeys at Sacramento Zoo, for example, were found to threaten members of the public significantly more often than they threatened keepers (Mitchell *et al.* 1991b). Furthermore, adult male mangabeys directed the same number of threats to non-human primates in neighbouring cages as they did to keepers (adult females and juveniles directed more), allowing the conclusion to be drawn that the monkeys treated keepers as familiar conspecifics.

Do different keepering styles result in different animal–human relationships, with resulting consequences for well-being, in the zoo as they do on the farm? Hardly any research has been done on this, but a study by Mellen (1991) suggests that they do. She was investigating the inconsistent breeding success of small cats in zoos and measured fifteen variables in eight different zoos to see which ones correlated with breeding success. One of the findings was that reproduction was more successful in cats where their keepers spent time talking to them and interacting with them (but see **Box 13.2**).

Box 13.2 **WHAT CAN HAPPEN WHEN THE HUMAN–ANIMAL RELATIONSHIP GOES WRONG**

We know hardly anything about the relationships between keepers and their animals, or the consequences for the well-being of either party. However, keepers are well aware that even the smallest and most innocuous-looking of animals can cause them some damage if they choose to, and some, such as venomous animals, constitute an obvious risk to which a number of keepers succumb every year, though thankfully not with serious consequences (Vohra *et al.* 2008). So the possibilities for establishing relationships are constrained to some extent by safe working practices. Can these practices damage the relationship with the keepers?

Once again, we do not know the answer to this question. However, we do know that in the case of elephants attacks on keepers do occur, sometimes with fatal consequences. Gore *et al.* (2006) have analysed the details of 122 elephant-related injuries to keepers and visitors between 1988 and 2003, along with other reports from the literature. Fairly obvious features, such as the

animal being in pain or a bull elephant being in musth, only accounted for a very small number of cases. Similarly, the inexperience of the keeper or the procedures that the keeper was doing at the time also accounted for only a small number of cases. Attacks were mostly initiated by female elephants, but that may be because there were more female than male elephants in the zoos. Nevertheless there were indications that females older than 20 years could be a particularly dangerous group, because they may not have shown previous aggression and therefore keepers would not anticipate an attack.

Gore *et al.* (2006) looked at a number of animal-related, management-related, and keeper-related factors that could have influenced the likelihood of attack, but no single factor was clearly implicated. This sort of study is rare, but important, if we are to properly understand the keeper–animal relationship and its consequences for the well-being not only of the animals, but also of the keepers.

Again, as with farm and laboratory animals, the management and handling of animals can be influenced by the stockperson skills of the keeper (**Fig. 13.23**). Carlstead (2009) analysed keeper ratings of how they behaved towards the animals, and how the animals behaved back to them, across four different species: the black rhinoceros *Diceros bicornis*, cheetah *Acinonyx jubatus*, maned wolf *Chrysocyon brachyurus*, and great hornbill *Buceros bicornis*. She found differences in fear and in affinity of different animals towards their keepers depending on the particular management and handling styles of the keepers. Few observational studies have been undertaken in this area, but one found that positive relationships of black rhinoceros with their keepers at Paignton Zoo Environmental Park resulted in low **latencies** of the animals doing what their keepers ask them to do—that is, the animals responded more quickly to their keepers (Ward and Melfi 2004). As with

farm and laboratory animals, it appears that very close relationships can be set up between animals in zoos and their keepers (**Plate 13.2**), at least as perceived by the humans (Hosey and Melfi 2012).

Figure 13.23 Keepers are in regular intimate contact with their animals, and their stockperson skills can influence how comfortable the animals are in their presence. (Photograph: Jeroen Stevens)

However, we must remain cautious about assuming that the animals perceive the relationship in the same way as we do (Hosey 2013). Some empirical evidence suggests that behavioural change, at least in gorillas and chimpanzees, can simultaneously indicate both increased arousal and decreased stress as a result of increased interaction with keepers (Chelluri *et al.* 2013), which makes interpretation a little ambiguous.

The combination of familiar and unfamiliar people

When we look at the agricultural literature, we can see that the quality of the relationship set up between the animals and their stockperson is of great importance, and can affect the behaviour of both, and ultimately, at least for the animals, their welfare and life history. We would expect this to be true of zoo animals as well and, although there is very little evidence, what there is suggests that this is, indeed, the case.

But zoo animals, as we have seen, also encounter plenty of unfamiliar people who come as zoo visitors, and their responses to these are quite variable. Could it be that the quality of relationships that zoo animals have with their keepers influences the way in which the animals respond to visitors? Hosey (2008) has suggested that this is the case. Effectively, zoo animals develop a relationship with the generalized group 'zoo visitors' and this interacts with the relationship they have with their keepers to influence the way in which the animal responds to both. Agricultural animals that have good-quality (positive) relationships with their stockpersons have low fear and some confidence with people, whereas those with poor-quality (negative) relationships show high fear of humans and avoidance of contact (Waiblinger *et al.* 2006). In between these is a neutral relationship, in which the animal has low fear of humans, but still avoids contact. If we apply this to the zoo setting and incorporate the two different sorts of humans (familiar and unfamiliar) that these animals encounter, then we get the sorts of characteristics that we see in **Fig. 13.24** (Hosey 2008).
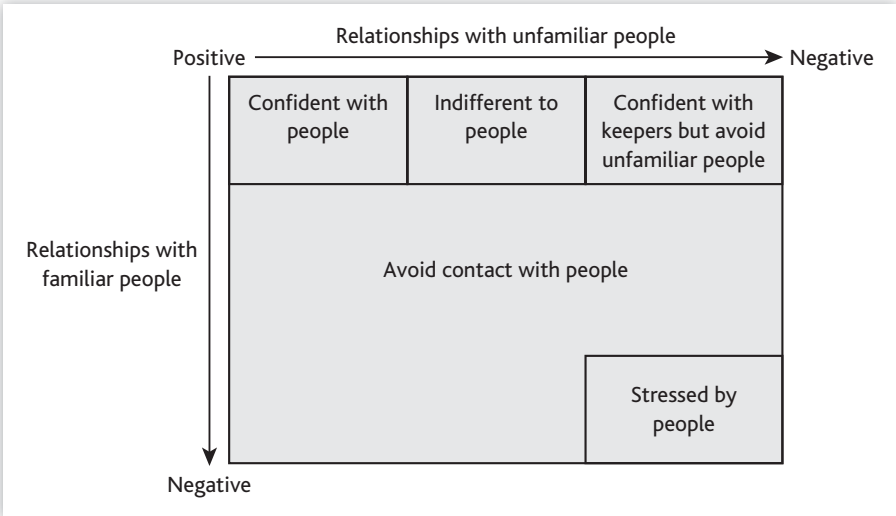
Figure 13.24 If we assume that zoo animals set up particular relationships with their keepers (familiar people), but have a generalized relationship with unfamiliar people (such as zoo visitors), then we could predict that the quality of those relationships (how positive or negative they are) has consequences for how the animal responds to the presence of people. Clearly, the best scenario for the animal is positive relationships with both familiar and unfamiliar people. (Figure based on Hosey 2008)

If this way of looking at human–animal interactions is supported by future studies, it may help us to improve the relationships that zoo animals have with visitors as well as keepers. As an example of how this might work, we can point to a study that we have already mentioned—that undertaken by Melfi and Thomas (2005) of colobus monkeys at Paignton Zoo Environmental Park. These animals were trained (see **section 13.4**) to undergo oral examination. After training, their interactions with the public declined. Similarly, when gorillas *Gorilla gorilla* at Barcelona Zoo were given additional training and playing therapy, their affiliative behaviours increased and aggression and stereotypies decreased, but there was also a reduction in their interactions with the public (Carrasco *et al*. 2009). Positive reinforcement training is widely thought to increase the quality of the animal's relationship with its keeper (Bassett *et al*. 2003; McKinley *et al*. 2003), so its use in zoos might yield the additional benefit of making the animals less responsive to visitors.

13.4 Training

Of course, all captive animals have to be handled occasionally for purposes such as medical treatment, routine veterinary procedures, transportation to other housing, and so on. The studies on farm and laboratory animals suggest that such handling is generally stressful for the animals.

Stress related to handling can be reduced in various ways, although the simplest method is for handlers to be calm and quiet during handling. If the animals associate positive consequences (such as gentle patting or stroking) with being handled, this can, over time, reduce the degree of fear and aversion they feel towards handling (LeNeindre *et al*. 1996). Effectively, the animal learns through experience that handling is positive or neutral. By this means, positive or neutral relationships can be set up between the animals and their stockperson (Hemsworth

2003; Waiblinger *et al*. 2006), as discussed in **section 13.3.4**. Direct handling is not usually a feasible or appropriate course of action for zoo animals because, for many species held in zoos, this would be potentially dangerous for both the keepers and the animals, or may compromise their 'role' within the collection. There are also some concerns that too much handling or exposure to humans could have a detrimental effect on the behaviour and/or the breeding of zoo-housed species (see **Chapter 6**). Little research has been done on the effects of handling on zoo animals, but one study implies that it might not lessen stress, even if behaviour changes. Regular handling of wombats *Lasiorhinus latifrons* does reduce their flight distances and behavioural reactivity, but their faecal cortisol levels do not reduce (Hogan *et al*. 2012). This emphasizes that the relationship between human contact and animal well-being is complex, and might be different in different species.

This effect of handling is probably one of the simplest forms of training. Training is considered to occur when we (humans) determine what animals learn (Mellen and Ellis 1996). As explained in **Chapter 4**, **learning** occurs when an event increases or decreases the likelihood of a behaviour being repeated in the future. In zoos, we are constantly manipulating the animals' environments and thus influencing which behaviours they will perform in the future. This happens in an informal way, through daily husbandry, and is sometimes referred to as 'passive training', because the animals' behavioural expression is not predetermined by trainers, but occurs as a consequence of the animals' learning something about human activity. Zoo animals are continually learning about their environment; for example, an animal may learn to associate the noise of keys with the approach of a keeper, or the sight of a keeper with a wheelbarrow of food with feeding time (Young and Cipreste 2004).

A more formal approach to changing animal behaviour, or 'active training', can be achieved by eliciting the desired behaviour through

appropriate and planned changes to the animals' environment or human–animal interactions. For example, if we were to want an animal to come inside at night, we could start by ensuring that all keepers showed the animal some food in the evening and then left the food inside; this is referred to as luring. The animal would quickly learn to come inside to get access to the food.

13.4.1 Positive reinforcement training

There are many ways in which humans can manipulate what an animal learns, not least by influencing the environment and thus the **stimuli** to which the animal is exposed on a daily basis. The basic underlying principles of learning theory are explained in **Chapter 4** and, when these are understood, they can be used to modify zoo animal behaviour (e.g. Ramirez 1999; Pryor 2002; Laule *et al.* 2003). The most frequently used methods to train animals in zoos are based on operant conditioning techniques; simply reinforcing a behaviour will increase the likelihood that it will occur again in the future. If the animal avoids or moves away from the stimulus (e.g. an ankus in elephant training), this is termed negative reinforcement training; if the animal moves towards the stimulus (e.g. a target when 'shaping' a behaviour), this is

known as positive reinforcement training (PRT). However, if a behaviour is ignored or punished, it will be less likely to occur. Steve Martin, an influential and experienced trainer in this field, talks about '*setting animals up to succeed*', by which he means that, if you act appropriately, you should only need to reinforce your animal and then reward it for performing the appropriate behaviour, rather than punishing the animal for performing a behaviour you do not want to see.

The degree of complexity inherent in training varies. One of the simplest forms of training is to 'capture' a behaviour that you want to see again in the future; when you see the behaviour that you want the animal to show, you reinforce it. If the behaviour you want to see does not currently exist in your animal's behavioural repertoire, you can reinforce successive approximations to the behaviour—a process called 'shaping' (**Fig. 13.25**). Thus, any slight change in the animal's behaviour that is a bit more like that which the trainer wants is reinforced. Alternatively, if you want to deter a behaviour from being expressed or if the behaviour expressed does not take the animal in the required behavioural direction, you can withhold the reinforcement (punish), or else reinforce a mutually exclusive and alternative behaviour.

Figure 13.25 Shaping an open-mouth behaviour in an Abyssinian colobus *Colobus guereza* so that a dental check could be performed without catching, handling, or separating the animal from the group. The first step was to reward the animal for stationing (that is, staying at a designated stop); then the animal was rewarded for touching a target (the wooden spoon); the animal was then rewarded for keeping in the same position and moving its other hand to the target; eventually, a grape was shown to the animal, which opened its mouth, and the behaviour was captured. Each behaviour requires a cue that the animal understands and which is always provided consistently. Verbal commands can be added while training or afterwards. (Photographs: Vicky Melfi)

Reinforcers and punishments can take many forms, depending essentially on the animal's preferences. A good reinforcer is something that the animal likes a lot and for which it will 'work'. Unsurprisingly, food is often used as a reinforcer, but, for some animals, access to something they like (for example, a toy) or simply being given a scratch can work just as well. Similarly, a 'punishment' only needs to be something that the animal will avoid. Despite the term, punishments are not necessarily painful, but can simply be a 'time out'; for many animals, removing attention given by their keeper (caregiver) from them is something that they will try to avoid—although some individuals may, in fact, find this reinforcing.

To be able to train, you need to understand the subtleties of the individual that you are training, because individual, as well as species, differences will affect training. At the Bronx Zoo, for example, it was found that tamarins in general (not lion tamarins) were more rapid in approaching trainers and learning behaviours than some other South American species, such as marmosets, grey titis *Callicebus* spp., and pale-headed sakis *Pithecia pithecia* (Savastano *et al*. 2003). Similar results were found when training **callitrichids** at Paignton Zoo Environmental Park (Jago *et al*. 2006).

Many trainers use a secondary or conditioned reinforcer, such as a whistle or a clicker (any sound or cue that is not used in the animal's daily routine is suitable), which tells the animal that it has made the correct response and that the primary reinforcer (reward) is on its way. Again, the theory behind this is explained in **Chapter 4** (see particularly **Fig. 4.5**). However, the secondary reinforcer is only effective if it is used consistently, honestly, and immediately after the behaviour that it is intended to reinforce.

13.4.2 Should we train zoo animals?

Whether zoo animals should be trained or not is debated, with each side of the argument suggesting that there are potential benefits and problems associated with its practice; some of these are listed in **Table 13.2**. However, there are few **empirical studies** that have evaluated the impact of training on zoo-housed animals, and much of this debate is based on anecdotal evidence (e.g. Desmond and Laule 1994).

Training has been used in zoos to modify the behaviour of animals for many reasons, including husbandry, conservation and **reintroduction**, research, presentations, and education (see **Box 13.3**). The application of training, in any field, should only be attempted by competent staff, and when a need and the required goal behaviour have been identified. There are also some other notes of caution, which are expanded upon in **Box 13.4**.

There are no boundaries to which species can be trained; there are reports of success in training

Benefits	Disadvantages
1) Facilitates husbandry	1) Increases domestication of zoo animals
2) Improves animal health and welfare	2) Can be too invasive (e.g. ultrasonography)
3) Is enriching	3) May alter the animal's behaviour outside the training session:
4) Enhances human–animal interactions	a) reduces the conservation value of the animal
5) Improves reintroduction success of released animals	b) increases animal–human interactions
	c) affects animal–animal interactions

Table 13.2 Some arguments given for and against training zoo-housed animals

Box 13.3 WHAT CAN BE ACHIEVED THROUGH TRAINING?
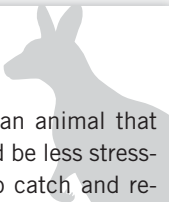
Historically, the goal of training animals has been for performances to entertain people. Nowadays, changes in visitor attitudes have meant that many 'traditional' animal performances, in which animals are trained to act like 'little people' or to do tricks, are not so well received and may portray a stereotype of the animal that is inappropriate in today's culture. For example Ross *et al.* (2011) found that there was an increased likelihood that people who viewed images of chimpanzees with a human standing in close proximity, or in a human setting, would consider wild chimpanzee populations to be stable/healthy.

However, Anderson *et al.* (2003) found that simply performing husbandry training while an interpreter was present to explain to visitors what was happening (that is, a performance), when done well, improved visitors' perceptions of the zoo, provided them with a greater insight into the animals, and meant that they actually stayed longer at the zoo. Other presentations that highlight animals' innate abilities, or portray a conservation or environmental message, are now commonplace in many zoos. Lukas *et al.* (1998) also point out that training sessions in zoos provide a great and effective opportunity for teaching students about the principles of operant conditioning theory.

A broad array of training is implemented for husbandry purposes. Intuitively, we would expect that taking blood samples from an animal that offers up its arm voluntarily would be less stressful for the animal than having to catch and restrain it, and then take the blood forcibly. This does, indeed, appear to be the case. Reinhardt (2003) found that the mean cortisol concentrations for six laboratory-housed rhesus monkeys *Macaca mulatta* were significantly higher when they were not trained, compared with when they were trained (see **Table 13.3**).

Similar results have been described in bongo *Tragelaphus euryceros*, where trained animals had significantly reduced cortisol levels when restrained in a box for 20 minutes, compared with untrained wild **ruminants** and even domestic cattle which were unused to handling (Grandin 2000). Training has been used to medicate individuals within a social group (for example, providing a wormer to Abyssinian colobus *Colobus guereza* (Melfi and Poyser 2007)) to facilitate **artificial insemination** in Asian rhinoceros *Rhinoceros unicornis* (Schaffer *et al.* 1990); to do the same in gorilla *Gorilla gorilla gorilla* (Brown and Loskutoff 1998); and to teach parenting skills in the giant panda *Ailuropoda melanoleuca* (Zhang *et al.* 2000).

Operant conditioning techniques have also been used to aid conservation goals, especially those of reintroduction.

Blood sampling procedure	Mean cortisol concentration		Difference (significance)
	First sample	**Second sample**	
Traditional	20.1 $\pm$ 4.5 µg/dl	33.8 $\pm$ 5.3 µg/dl$^-$	$p < 0.001$
Trained	19.6 $\pm$ 3.0 µg dl^{-1}	22.3 $\pm$ 5.0 µg dl^{-1}	$p < 0.1$

Table 13.3 Mean cortisol concentrations measured in six laboratory-housed rhesus macaques, after blood sampling using the traditional restraint method and after the macaques had been trained to 'cooperate' with blood sampling*
*Data from Reinhardt (2003).

most zoo-housed species, from primates to pinnipeds, crocodiles to cetaceans, and beyond. For example, giant pandas have been trained to move within their enclosure (Bloomsmith *et al.* 2003), Aldabra tortoises *Geochelone gigantea* have been trained to stand while blood samples are taken from them (Weiss and Wilson 2003), and many other reptiles have been trained for veterinary procedures, whether in zoos or kept as pets (Hellmuth *et al.* 2012).

Box 13.4 CAUTIONARY NOTES ON IMPLEMENTING TRAINING IN ZOOS

Although training has become widely implemented in many zoos, there are few studies that have been undertaken specifically to test its impact on the behaviour and biology of the animal, other than the behaviour that is being trained. We have records of how many sessions it may take to train callitrichids in different tasks (Savastano *et al*. 2003), or which behaviours can be trained, but we have little understanding of how the training process may affect these individuals or the dynamic of the social group. This does not necessarily mean that training should be avoided or that it has deleterious effects, but it does mean that we do not fully appreciate all its consequences and therefore should work hard to address this.

It is important, then, that research is undertaken to explore and test the advantages and disadvantages associated with training zoo-housed animals. Melfi and Thomas (2005) were able to show that husbandry training did not significantly alter the **activity budget** or social behaviour of Abyssinian colobus monkeys. But it did affect the frequency of monkey-initiated interactions with people over the period during which they were trained. **Figure 13.26** illustrates that, as the training process progressed, they interacted less and less with people (see also **section 13.3.4**). Therefore training can clearly have effects on behaviour other than those that are planned.

The majority of training implemented in zoos is for husbandry purposes and requires the animals to learn that certain procedures are not to be feared. This can be particularly beneficial when the alternatives can be dangerous; for example, training animals to station (that is, to remain immobile in a particular spot) can negate the need for physical and/or chemical restraint (Wardzynski *et al*. 2005). Modification of 'undesirable' behaviours is also attempted in some situations. Bloomsmith *et al*. (2007) have suggested that operant conditioning techniques could be used to limit stereotypies and self-injurious behaviours in non-human primates.

In other situations, non-human primates have been trained to react to social situations in an uncharacteristic way. For example, high and low socially ranked macaques were trained to initiate fewer and more social interactions (Schapiro *et al*. 2003), respectively, and a dominant male chimpanzee was trained to remain still while the rest of his group ate freely around him (Bloomsmith *et al*. 1994). In these situations, the need for data to clarify what impact training has on the animal is very important. It is possible that training can modify an animal's behaviour, but, if the environmental stimuli or the animal's internal motivation do not change, then the animal may be frustrated between the behaviour that it is 'motivated' to perform and the behaviour that it has been trained to perform (see **section 4.1.3** for more on motivation). If this is the case, training may function as a mental barrier to behaviour performance, in much the same way that physical barriers have previously been used to stop animals pacing.
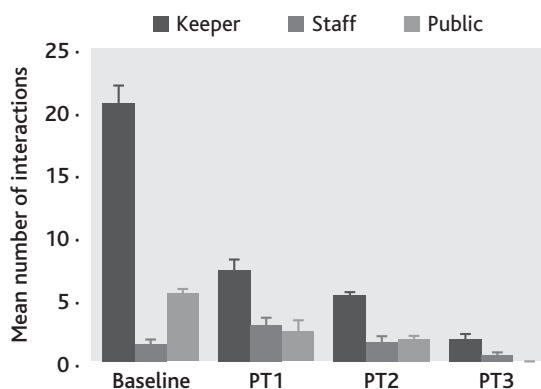
Figure 13.26 A training programme at Paignton Zoo Environmental Park, which aimed to achieve oral examinations of Abyssinian colobus monkeys *Colobus guereza* without the need for catch-ups, had very little effect on the behaviour of the animals—but it did greatly affect how they interacted with people, whether zoo visitors or staff. The frequency of colobus-initiated interactions towards people, whether staff or visitors, declined significantly after training started. Baseline represented the period of time before training started, and data collection continued for the first month (PT1), the second month (PT2), and the third month after training (PT3). (From Melfi and Thomas 2005)

Summary

• Zoos worldwide are visited by huge numbers of people, who appear to come from all sectors of the population. They mostly visit the zoo for enjoyment and to see animals, and are generally positive about zoos.

• Zoos attempt to educate their visitors and change their attitudes through both informal (such as signs) and formal (such as keeper talks) means, but these seem to have limited success in changing attitudes and behaviour.

• There is evidence that zoo visitors affect the behaviour of some of the animals and, in some cases, this appears to be stressful for the animals; on the other hand, some animals are not affected at all and some even seem to be enriched by human presence.

• Keepers, in contrast, are likely to have a more intimate relationship with the animals, although very little is known about this.

• Training of animals allows routine husbandry to take place in what may be a less stressful atmosphere for the animals and may have beneficial effects on their relationships with people as well.

Questions and topics for further discussion

1. What educational messages should zoos be trying to convey to their visitors?
2. Should zoos use some of their animals for demonstrations and displays?
3. 'When zoo animals have been trained or used in public demonstrations, they are no longer representative of their wild counterparts.' Is this true—and does it matter?
4. If keepers have close relationships with zoo animals, does this help or interfere with their ability to undertake routine husbandry procedures with those animals?
5. Should zoos ensure that paying visitors have good views of the animals or should the animals be provided with opportunities to hide from people?

Further reading

The study of visitor behaviour, attitudes, and education is now quite a sizeable area of research, and a comprehensive bibliography of publications in this field is provided by Schramm (2011). A useful set of perspectives on tourism as applied to zoos can be found in Frost (2011), although some of the contributions need to be approached rather critically. A summary of zoo conservation education, admittedly with somewhat of a North American bias, is provided by Routman *et al*. (2010). Heini Hediger's books (e.g. Hediger 1955; 1970), now long out of print, are still worth reading as an anecdotal account of the complex relationships between humans and zoo animals. A good account of the role of animal learning and training in the zoo environment is given by Mellen and MacPhee (2010).

Websites and other sources of useful information

If you are interested in studying human–animal interactions further, there is a society devoted to that cause; the International Society for Anthrozoology (**http://www.vetmed.ucdavis.edu/CCAB/isaz.htm**) organizes conferences and publishes the journal *Anthrozoös*.

Those who are sufficiently motivated to undertake their own research in the area of human–animal interactions in the zoo are advised to read the research guidelines by Mitchell and Hosey (2005), which are available at the BIAZA website (**http://www.biaza.org.uk**).

For those wishing to take their knowledge and expertise of training further, the Animal Behaviour Management Alliance (ABMA) (**http://theabma.org/home.asp** provides information and help to members.

Zoo education is now a large and innovative field, and a good place to see what is being done is the web page of the International Zoo Educators Association (**http://www.izea.net**) on which news,

information, and online access to the Association's journal are available.

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.
http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Chapter 14
Research

Research is about finding out new things and is also about solving problems. Zoo research can lead to important new information that stretches the boundaries of science, but, equally, it can be about finding the best way to deal with difficulties that have arisen in the day-to-day running of the zoo. Research in zoos is not only about animals; researchers may be interested in collecting data on the economics of zoos as commercial enterprises, or on the ability of zoo grounds to support local biodiversity. Indeed, zoo research covers a spectrum from biology, through physics and chemistry, to psychology and sociology, and beyond. But because this book is about zoo animals, rather than zoos *per se*, this chapter concentrates on research carried out by and within zoos on the biology and behaviour of captive animals.

Zoo animal research poses some particular challenges in comparison with other areas of biological research. These include problems of **confounding variables**, small sample sizes, and a possible lack of independence of data points, which are of wider interest in their own right, because of the methodological problems that they present. Other aspects of zoo research can experience similar problems to research on laboratory or farm animals, or animals in the wild.

In this chapter, we will consider the following points.

14.1 Why is zoo research important?
14.2 What is 'research'?
14.3 What is 'zoo research'?
14.4 Some methodological difficulties in zoo research
14.5 Problems in the analysis of data
14.6 Multi-zoo studies
14.7 Disseminating the results of zoo research
14.8 What zoo research still needs to be done?

There are also boxes dealing with some of the conceptual and methodological issues that arise from zoo research.

The chapter deals primarily with behavioural research, which is probably the area in which most student research is carried out, and in which there are particular issues to do with sampling and data analysis. However, these issues can be dealt with, as is explained further in this chapter. The chapter should provide a framework for understanding and interpreting the results of zoo research, and also a basis for developing research skills in the zoo environment.

14.1 Why is zoo research important?

Research in any scientific discipline is often characterized as being either 'basic' (sometimes also referred to as 'pure' or 'fundamental'), which is to do with advancing theory and discovering knowledge for its own sake, or 'applied', in which case the research is designed to solve a practical problem or to help a process to perform better. Both of these are of enormous importance in the zoo context.

The zoo environment is a unique one in which to study animals. Unlike the wild, the animals are relatively accessible to the researcher, so data can be collected from zoo animals that would be logistically very difficult to get from their wild counterparts. Furthermore, zoo research is a considerably less expensive way of getting data on exotic species than fieldwork in the animals' natural habitat and yet the results of research on animals in zoos can give useful insights into the biology of their wild-living counterparts.

This has led to discoveries such as the presence of political behaviours in chimpanzees *Pan troglodytes* (de Waal 1982)[1], tool use in a fish, the sixbar wrasse *Thalassoma hardwicke* (Paśko 2010), and **parthenogenesis** in Komodo dragons *Varanus komodoensis* (Watts *et al.* 2006)[2] (**Fig. 14.1**). Hutchins (2001) cites other examples of zoo-based research that has shed light on the basic biology of species, such as the reproductive physiology of killer whales *Orcinus orca*, for which data would be very difficult to collect in the wild.

Again unlike the wild, some manipulations may be possible in the zoo to take research beyond purely observational and into experimental approaches. The zoo environment is similarly different from that of the laboratory. In most cases, the animals studied in the zoo live in much more naturalistic groups and enclosures than any that might be studied in a laboratory. Because of this,

Figure 14.1 Parthenogenesis has been discovered in the komodo dragon *Varanus komodoensis* in zoos. This would have been difficult to demonstrate in the wild. (Photo: Geoff Hosey)

the data collected from zoo animals can have greater biological relevance than that obtained from the laboratory and can tell us more about what these animals are like outside the captive environment. Add to this the fact that zoos are full of interesting animals, many of which have not been extensively studied and many of which are endangered (**Plate 14.1**), and you can argue that the zoo is a suitable place in which to conduct basic biological research.

In fact, zoos have a long history of research into aspects of animal biology, even if this was not the primary purpose for which they were established (Hutchins 2001). For example, the Zoological Society of London's founding charter refers to the need for a '*collection of animals … to be applied to some useful purpose, or as objects of scientific research*'. On the other side of the Atlantic, the New York Zoological Society founded the Department of Tropical Research in 1916 and the Institute of Animal Behaviour Research in 1966.

What about applied research in zoos? Problems that may affect the welfare, **nutrition**, health, or other features of the animals' lives in the zoo benefit from the application of scientific research methodology. By this, we mean a systematic approach that makes hypotheses about the possible

---

[1] This research was undertaken by a University of Utrecht researcher at Burgers' Zoo in Arnhem, The Netherlands.

[2] Researchers from the University of Liverpool, University of Florence, Chester Zoo, and ZSL.

causes of the problem and then collects data to identify which of the possible hypotheses is most likely to be correct. This empirical approach is far more powerful than unsystematic trial-and-error approaches, because it provides information from studies that are repeatable elsewhere, rather than only anecdotes. This, then, provides data that can be used by the team of animal managers in the zoo to decide on appropriate courses of action to solve or alleviate any problem occurring. For example, is the **enrichment** provided effective? How much of the food provided is digested? As such, applied research is an essential component of zoo management.

14.2 What is 'research'?

The question of what 'research' actually is may not be as easy a question to answer as we might at first think. One definition, used by the UK Government in its evaluation of research[3] undertaken by universities and other higher education institutions, is that research is '*original investigation undertaken in order to gain knowledge and understanding*'. This is largely concordant with the description given in the World Zoo and Aquarium Conservation Strategy (WZACS) (WAZA 2005), that research in zoos and aquariums should be aimed at accruing new knowledge to help the zoo to improve its operations or to further science (basic and applied animal research).

None of this seems particularly contentious, but it is important because zoo critics interpret research in a rather stricter way than do members of the zoo community. The Secretary of State's Standards of Modern Zoo Practice (Defra 2004), for example, which aims to help zoos interpret just such things as this (see **Chapter 3**), tells zoos that '*at the minimum this* [research] *need constitute no more than collecting and collating information for statistical purposes*'. But critics such as

Rees (2005b) maintain that this routine record keeping is not research.

This might be true in a technical sense if these records are not reviewed, but the records that are kept can also be seen as data and the statistical analysis of these data[4] is research (see **Chapter 5**). For many small zoos and aquariums, this may be a realistic way in which to contribute to research, and the data collected can be, and are, analysed by others to contribute new knowledge (**section 14.3.5**). Indeed, such analyses contribute to the evidence base which is important for housing and husbandry.

14.3 What is 'zoo research'?

It is probably best to remain relatively flexible about the definition and scope of zoo research, and to regard it as any activity that increases our knowledge and understanding of animals and their environment, whether it be zoo or wild. So, what are the characteristics of zoo research?

14.3.1 What is zoo research for?

As we mentioned above, WZACS (WAZA 2005) sees the function of zoo research as helping the zoo or the researcher to achieve his/her goals. What they mean by this is that research should be conducted to help in furthering the operations of the zoo, to help zoos achieve their mission and vision (see **section 2.5**), and to increase knowledge and improve practice in things such as captive breeding, conservation, welfare, and so on, and also that zoos should facilitate research (by providing access to animals, biological samples, and such things, as long as this does not interfere excessively with husbandry, reduce welfare, or infringe legal requirements) for university and other researchers to do comparative biological work. Another way of looking at this is that we would expect a lot of the research undertaken in zoos to

---

[3] This refers to the Research Assessment Exercise (RAE), periodically undertaken by the Higher Education Funding Councils for England, Scotland, Wales, and Northern Ireland.

[4] A reminder here that the word 'data' is a plural, so 'data are' is correct, rather than 'data is' although nowadays 'data is' is very commonly used, even by the BBC

be applied—that is, designed to provide results that can be used to improve the captive management of animals—but that basic research in zoos, designed to advance knowledge for its own sake, should also be possible and encouraged.

14.3.2 How much research is done in zoos?

The undertaking of research is an important part of zoos' conservation strategies and other mission statements (see **Chapter 10**). Indeed, under the EC Zoos Directive of 1999 (see **Chapter 3**) it is a legal requirement in the UK that zoos are involved in research,[5] particularly research that helps to achieve the conservation objectives of zoos. So how much research is actually done in zoos, and is it increasing in response to strategies and directives such as these?

This is not an easy question to answer, for a number of reasons. A great deal of research in zoos is conducted by students (for example, as undergraduate and postgraduate research projects or as part of placements) (**Fig. 14.2** and **Plate 14.2**) and volunteers. For example, Chester Zoo may support as many as 200 researchers, many of whom are

Figure 14.2 A research student analysing faecal samples from Zoo Planckendael (Photograph: Jeroen Stevens)

---

[5] This requirement comes from the EC Zoos Directive 1999/22/EC (see **Chapter 3**).

undergraduates, working there annually, and Paignton Zoo often supervises up to forty or fifty students every year. This provides an excellent training opportunity for the students, and results in the collection of data and other outcomes that can be valuable to the zoo—but these studies are rarely published in the peer-reviewed journals (see **section 14.7**). So simply looking at the published outcomes of zoo research is likely to underestimate the amount of research-related activity that actually goes on.

An alternative way of finding out how much research zoos do is to ask them. Here, again, we are likely to underestimate the true amount of research. We have only to think of the analyses of routinely kept records referred to in the previous section; many zoos may consider that this is not an example of their research, simply because the analysis is done by someone from a different organization. Then again, researchers from universities who use zoo facilities are not necessarily engaged in collaborative research and so may not be counted by a zoo as part of their research effort.

However, some surveys of zoo research have been undertaken. One of the earliest was that of Finlay and Maple (1986), who analysed replies by 120 AZA zoos and aquariums to a questionnaire. Seventy per cent of these reported that they had recently been involved in research, and 46 per cent said that their research programmes were expanding. However, only 27 per cent of them had a research committee or research department, and an even smaller number of them (21 per cent) had written research guidelines. Most of the research was being undertaken by larger zoos or aquariums, mostly on behavioural and reproductive biology, and mostly on non-primate mammals. Those zoos and aquariums that were not involved in research tended to give 'lack of funds' and 'lack of trained staff' as the principal reasons for this fact. Nevertheless, for the time, this was a respectable level of research activity.

A repeat of this survey 12 years later (Stoinski *et al.* 1998) found that research activity had increased (88 per cent of 123 responding zoos and aquariums), but many of the findings of the earlier survey were still being reported. Thus, it was still the

larger zoos and aquariums that were involved in research, and lack of funds and staff were still being cited as the major reasons for no involvement in research. But 64 per cent of the zoos surveyed now had written guidelines, and 90 per cent had either a research committee or a research department (or both). These authors concluded that research was 'alive and well' in zoos and aquariums, but that there was still room for improvement because the majority had no staff employed solely for research and fewer zoos than in the 1986 survey reported that their research was expanding.

A brief survey by Nogge (1997), which received replies from fifty-seven European zoos, found that 73 per cent of these were involved in research, again mostly in ethology (34.1 per cent of projects), reproduction (15.5 per cent), conservation (12.4 per cent), and veterinary medicine (12.4 per cent). However, surveys as detailed as that of Stoinski *et al.* (1998) do not appear to have been published for the UK, or for Europe as a whole, or indeed for the rest of the world, so it is difficult to identify any trends. What we can say is that, in the past ten years, research outcomes that have appeared through the work of the Research Committee of the British and Irish Association of Zoos and Aquariums (BIAZA) (see **Box 14.6**) have increased enormously, suggesting again that there is a sizeable (growing?) research effort in zoos within the Association's area.

14.3.3 What sort of research is done in zoos?

As mentioned earlier, zoos offer opportunities for research in many different scientific disciplines, as well as the social sciences. Almost all areas of biological investigation can be studied in the zoo setting, and **Table 14.1** shows the range of topics that can be covered and the interrelationships between them.

In general, these can be divided into three categories:

- basic and applied studies of topics such as behaviour, physiology, genetics, nutrition, welfare, wildlife medicine, and so on (**Fig. 14.3**);

Figure 14.3 Zoos give researchers access to many species of animals that would be difficult to achieve elsewhere. Here, a researcher gathers vocalization data at a primate enclosure. (Photograph: Whitley Wildlife Conservation Trust)

- field-based conservation research;
- operational research about the zoo itself, and how its roles and procedures can be improved.

But although all of these things can be, and are being, investigated, we can nevertheless ask where most of zoo research is actually being directed.

The two American surveys mentioned earlier asked the zoos and aquariums what their major topics of research were. In the 1998 survey (Stoinski *et al.* 1998), the top areas of study were behaviour (85 per cent of respondents), reproduction (75 per cent), visitor studies (67 per cent), and husbandry (66 per cent). An alternative way of getting this sort of information is to look at the profile of zoo-based publications in major scientific journals. Kleiman (1992) analysed the papers published by the journal *Zoo Biology* between 1982 and 1990, and found that only 28.4 per cent of them were behavioural, with the rest divided between management (26.2 per cent), reproduction (19.6 per cent), biomedical (18.2 per cent), genetics (5.1 per cent), and nutrition (2.6 per cent). She also found that, during this period, applied research papers increased and basic research papers decreased in number in the journal.

Topic	Anatomy and morphology	Biogeography	Ecology	Education	Ethology	Genetics	Nutrition	Physiology	Population biology	Social science	Systematics and taxonomy	Veterinary medicine
Ageing	✗		✗		✗	✗	✗	✗	✗			✗
Animal welfare	✗		✗		✗		✗	✗				✗
Behaviour			✗		✗	✗	✗	✗				✗
Biomaterial banking		✗				✗			✗		✗	✗
Biotechnology	✗					✗	✗	✗				✗
Contraception	✗				✗			✗				✗
Dietary studies	✗		✗		✗	✗	✗	✗	✗		✗	✗
Disease	✗	✗	✗		✗	✗	✗	✗				
Domestication	✗		✗		✗	✗	✗	✗				
Environmental enrichment	✗		✗		✗		✗	✗				
Husbandry	✗		✗		✗	✗	✗	✗	✗			✗
Identification	✗				✗	✗		✗			✗	
Life history	✗	✗	✗		✗	✗	✗	✗	✗			✗
Population management		✗	✗		✗	✗		✗	✗		✗	✗
Reproduction	✗		✗		✗	✗	✗	✗	✗			✗
Taxonomy	✗	✗			✗	✗		✗			✗	
Visitor studies				✗	✗					✗		

Table 14.1 The range of academic disciplines that can contribute to research in zoos*

* From the WZACS (WAZA 2005).

Note: The topics in the left-hand column are those that much of zoo research covers; the crosses indicate the primary disciplines that are involved in researching those topics.

In a similar analysis, Hosey (1997) found that the proportion of behavioural papers in *Zoo Biology* had risen to 43 per cent in the period 1991–1994, and only about 40 per cent of these were non-applied.

Behavioural studies also dominate in a survey by Semple (2002) of 904 research projects in the Zoo Federation (now BIAZA) database. In this survey, behaviour and enrichment studies made up the majority, whereas topics such as nutrition (4.5 per cent of projects) and genetics (0.9 per cent) were significantly underrepresented (**Fig. 14.4**).
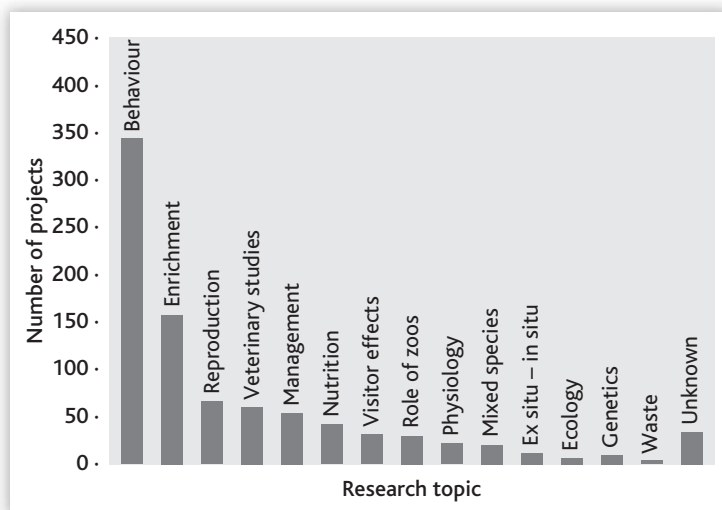
Figure 14.4 Topic areas covered by 904 research projects undertaken in BIAZA member zoos were collated in a database in 2002. There appears to be a bias towards studies of animal behaviour and enrichment. (From Semple 2002)

These results do not appear to be particularly concordant with the American surveys. There are probably many reasons for this. Firstly, *Zoo Biology* is only one of several journals that routinely publish results from zoo studies (see **Box 14.5**). Secondly, opinions sometimes differ as to which categories particular kinds of research should go into; for example, is an enrichment study to be regarded as research into behaviour, welfare, or husbandry? Thirdly, a large proportion of zoo research never gets published in the peer-reviewed journals. For example, Semple's (2002) survey includes a large number of student projects; in their survey, Stoinski *et al.* (1998) found that zoos preferred to publish their results in their own in-house publications or in conference proceedings. (We will return to this issue in **section 14.7**.) And finally, it is likely that more behavioural than other sorts of research is undertaken in British zoos simply because the legislation on working on animals is more restrictive, and there are fewer trained animals to obtain samples from.

A further question that we can ask is about which **taxa** are most frequently studied. In their survey, Stoinski *et al.* (1998) found a heavy emphasis on mammals. Thus, 63 per cent of their respondents were involved in research on **carnivores**, 50 per cent on **ungulates**, 41 per cent on great apes, and

47 per cent on other primates. Birds (53 per cent of respondents), reptiles (50 per cent), amphibians (21 per cent), and fish (26 per cent) received less attention. What this means in terms of amount of research is not clear (after all, the zoos involved in carnivore research might have only one project each, but those involved in birds might have a lot more), but there does seem to be an emphasis on research on the great apes, considering how few species there are in comparison with other taxa.

This is also the conclusion reached by Melfi (2005), who surveyed projects on primates in the BIAZA and American Association of Zoos and Aquariums (AZA) research databases (see **Box 14.6**) and found that hominids[6] accounted for a disproportionately large number of research projects in both the USA and the UK and Ireland (**Fig. 14.5**). More recent surveys by Anderson *et al.* (2008), which looked at 25 years' worth of papers in *Zoo Biology*, and Maple and Bashaw (2010), which analysed the results of a literature search, have confirmed a bias towards mammals generally, and carnivores, non-human primates, and ungulates in particular. One possible message for would-be zoo researchers is that there is a need to diversify—there are plenty of taxa that are simply not being studied enough.

---

[6] Hominids may sound as if they are people, but recent molecular analyses have led to the great apes being reclassified in the same family as ourselves, Hominidae.
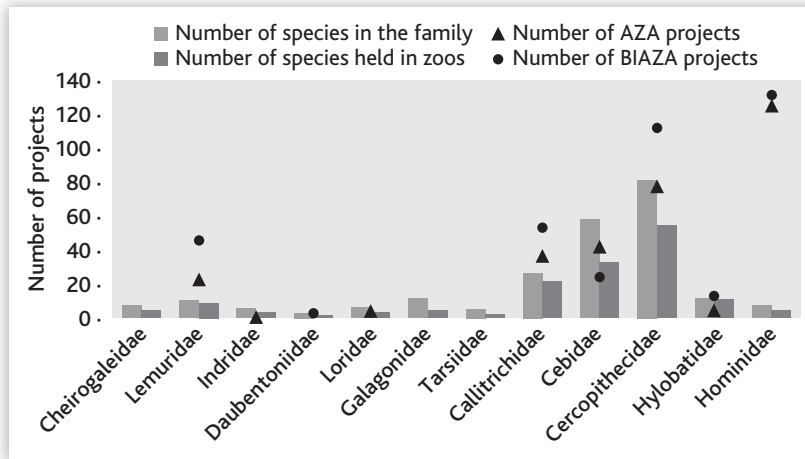
Figure 14.5 In this breakdown of 706 primate research projects on the AZA and BIAZA databases, it is clear that the number of great ape (Hominidae) projects is disproportionately high compared with the number of species, while some other families, such as South American primates (Cebidae) and gibbons (Hylobatidae), are under-represented. (Adapted from Melfi 2005)

14.3.4 Who does zoo research?

The American surveys discussed in **section 14.3.2** found that research tended to be concentrated in the larger zoos and aquariums, which had higher visitor attendance figures. It is likely that the same is true of other zoos. Research can be an expensive pursuit and requires investigators who are trained in the skills of research methodology. Potentially, this puts research out of the reach of many smaller establishments.

For these, and probably other reasons, many zoos undertake their research in collaboration with each other and with other agencies, such as universities and conservation agencies. Of course, it is also the case that some academics in higher education institutions are interested in zoo-based research and initiate the collaboration themselves. A growing number of academic researchers are now appreciating the value of zoos for research, which unfortunately has not always been the case.

Of 344 studies published in the journal *Animal Behaviour* in 1993 and 1994, for example, 163 involved captive animals, but only three of these were undertaken in zoos (Hosey 1997). Possible reasons why non-zoo behavioural biologists have avoided research in zoos are perceptions that zoo animals constitute abnormal populations, that **functional** theories of behaviour cannot be tested in zoos, and that there are just too many methodological difficulties (Hosey 1997). Hopefully, a reading of **Chapters 6–9** will convince the reader that the first of these objections is not necessarily true, but we will look more closely at this in **Box 14.1**.

Box 14.1 ARE ZOO ANIMAL POPULATIONS 'ABNORMAL'?

Suppose that we are interested in a particular species of **exotic animal**, or are interested in a particular theoretical problem in something such as behavioural biology. If we were to do our research at a zoo, to what extent would our results be rendered worthless, or at least suspect, because of the unnaturalness of the animals' environment?

This is a difficult question to answer. There is a long tradition of anatomical and physiological research being undertaken in zoos, presumably on the assumption that anatomy and physiology are not affected by captivity. This may not be the case, however; for example, tigers in zoo specimens have a different skull morphology than those from the wild, probably because of a

different diet and more grooming (Duckler 1998). But it is in behaviour that we would expect the greatest change (see **Chapter 4**, in which deviations from 'normal' behaviour are addressed more fully). So, at worst, our research data on the behaviour of zoo animals may be suspect because the animals live in an unnatural enclosure, are in groups with an unusual age or sex structure, may show **abnormal behaviours**, and may interact with people. At best, zoo research represents the study of a diverse array of animals in complex environments in semi-natural social settings, providing a unique insight into their biology and behaviour that would otherwise be restricted in their natural habitat, or adversely affected by the standardized and relatively barren conditions of laboratory settings.

Perhaps the best answer at the moment is that zoo enclosures have become much more naturalistic in the last couple of decades and that, in some studies, no differences have been found between animals living in these enclosures and those living in the wild (see **Chapters 4**, **7**, and **8**). We are also now amassing much more data about the precise ways in which individual components of the zoo environment affect behaviour (see **Chapter 4**), so there is more opportunity to build these into the experimental design as possible variables.

Finally, we can point out that even apparently 'wild' populations of many species today are actually also affected in various ways by human activity (Hosey 2005), so the zoo is by no means unique in potentially changing animals' behaviours. Therefore the message is: go ahead and do the zoo studies, but be as informed from the literature as possible about zoo environments and use this to interpret results appropriately.

In relation to the second objection, we can point to studies that have tested functional theories in zoos. An example is the study by Cooper and Hosey (2003), which used colour-manipulated photographs to test theories of female mate preference in a number of lemur taxa in UK zoos (**Fig. 14.6**). Such a study would have been extremely expensive and difficult to achieve in the wild.

In fact, even the third of these three objections (methodological difficulties) does not pose a real problem to zoo research, as we will see in **section 14.4**.

Indeed, there is much to be gained by university-based psychologists and biologists undertaking research in zoos (Maroldo 1978; Moran and Sorensen 1984). They have access to a range of exotic species that otherwise could only be studied at enormous cost, and the results of their research can be of great importance in furthering the conservation of endangered species. Indeed, universities and zoos can complement each other in what they can bring to research (**Fig. 14.7**) because, although they have a somewhat different focus, there are substantial areas of overlapping interest, for example in topics such as the control and

Figure 14.6 Here, you can see a female brown lemur *Eulemur fulvus* looking at a photograph of a male brown lemur in an experimental viewing box as part of a research project to investigate whether females prefer brightly coloured males. (Photograph: Vicky Cooper)

| Zoo provides | | University provides |

Taxonomy and evolutionary processes

Scientific expertise

Anatomical studies

Personnel, laboratory facilities, analytical and publication expertise

Diet and nutrition

Specimens and samples

Reproductive biology

Individual histories

Genetics and population management

Expertise

Pathology and disease investigation

Specialized resources

Education and visitor studies

Personnel for data collection, analyses and publication

Access to animals in appropriate settings

Ethological studies and comparative psychology

Figure 14.7 Zoo research can be facilitated by support from both zoos and universities, each of which provide different types of expertise, knowledge, and resources. (From WAZA 2005)

analysis of behaviour, conservation of endangered species, and education of students and the general public (Fernandez and Timberlake 2008). It is probably also worth pointing out here that a great deal of non-behavioural research on zoo animals, notably related to veterinary and animal health, is published every year in the scientific journals.

14.3.5 Research by zoo staff

More and more zoos are hiring dedicated scientists onto their staff to facilitate and conduct research, and in some cases these staff may constitute a research department of the zoo. The research they do may extend beyond the zoo grounds, to reserves

and field conservation, and include a myriad of topics, already explored in **section 14.3.3**. Each zoo will prioritize projects accordingly; this will be affected by the animals in the collection, the interests and expertise of staff, links to other organizations or field sites, what can be practically and financially accommodated, global priorities, and many other factors. Some research departments can become sizeable research units; examples include the Institute for Conservation Research of the Zoological Society of San Diego, the Center for Research on Endangered Wildlife at Cincinnati Zoo, and the Conservation and Science Department at the Smithsonian National Zoological Park, and collectively these departments in the United States

spend as much as $75 million on conservation and research annually (Maple and Bashaw 2010).

Collaborations

Much of the research coordinated by zoo research departments is undertaken by university students and provides training opportunities for new scientists. Training in research methods is also provided to other zoo staff, who are then also able to collect data and conduct research. Increasingly, links between zoo- and university-based researchers are expanding, with university departments being sited on zoo grounds, or zoos gaining university funding, or simply providing joint supervision or teaching opportunities.

For example, the Royal Zoological Society of Antwerp conducts research through its Centre for Research and Conservation, a zoo-based research team that has university partners and financial assistance from the Flemish government (Pereboom *et al.* 2011) (**Fig. 14.8**). In the UK, collaboration between four Scottish universities (Abertay, Edinburgh, St Andrews, and Stirling) and Edinburgh Zoo has resulted in the establishment at the zoo of a purpose-built centre (the Living Links to

Figure 14.8 Morphometric measurements being taken on an anaesthetized bonobo *Pan paniscus* as part of a research project on primate locomotion undertaken jointly by university and zoo researchers at Antwerp. (Photograph: Jeroen Stevens)

Human Evolution Centre) where primatologists from these universities, who form the Scottish Primate Research Group (SPRG), are able to study primate behaviour, and members of the public visiting the zoo can watch scientific research as it is done (Macdonald and Whiten 2011).

Routine data collection and zoo records

We mentioned earlier (see **section 14.2**) that the records routinely held by zoos about their animals can provide an excellent source of data for further research into aspects of the animals' biology. Records put into ISIS, for example, are used for zoo collection planning, and potentially could be used for more detailed genetic and demographic analysis (Flesness *et al.* 1995; Flesness 2003). For example, Whitford and Young (2004) analysed the records of ten representative UK zoos over a ten-year period to see what trends there were in the captive breeding of endangered birds, and were able to show that there was an increase during this period in the percentage of threatened species kept and an increase in the number of species in each World Conservation Union (IUCN) Red List[7] category that were being maintained in zoos. Information relevant to animal health can also be usefully derived from zoo records. Pizzi (2004), for example, was able to analyse records of over a thousand **post-mortem** examinations of penguins at Edinburgh Zoo (**Fig. 14.9**),

Figure 14.9 Penguins are very popular in zoos and have been maintained in collections for a long time. This means that extensive databases exist that can be used to carry out research to inform husbandry. (Photograph: South Lakes Wild Animal Park)

[7] There is more about the IUCN Red List in **Chapter 10**.

from a database spanning over 90 years, to identify major causes of **mortality** and any possible correlates. He found that *Aspergillus* infections, causing fungal air sacculitis (a disease of the air sacs), were the most common cause of death (38 per cent of all penguin deaths) and that male birds were twice as likely to die from this as females. At present zoo records are probably less useful for conducting retrospective behavioural analyses (Hosey *et al*. 2012), but making the collection and entry of these kinds of data more systematic would greatly increase their usefulness for this, too.

14.4 Some methodological difficulties in zoo research

In principle, undertaking research in zoos is no different to any other kind of biological investigation. Any research project should include clear testable hypotheses or research questions, defined variables and measures, and explicit procedures for collecting and analysing data. Nevertheless, zoo environments do pose some challenges to the researcher, and, in this and the next section,

we will try to identify the major ones and discuss how they can be resolved.

For those who are about to undertake zoo research, we strongly recommend following the advice given in the various BIAZA research guidelines (see **Further reading**).

14.4.1 Questions and hypotheses

Any research study should clearly identify what hypothesis it is designed to test, and this hypothesis should relate to a body of existing knowledge that effectively provides a theoretical context for the study.[8] Without this, the results of a study can be difficult to interpret.

As an example we can consider enrichment studies (**Fig. 14.10**) in which, potentially, there may be a number of different hypotheses. Enrichment may be provided to try to achieve a broad behavioural profile in the animal that is more like that seen in the wild; it may also be provided to bring about a more specific change, for example, in an attempt to reduce **stereotypies**, or because the animal is believed to be too inactive, or for all sorts of other reasons (see **Chapter 8**). Whatever the reason for the

Figure 14.10 Enrichment is a popular topic for undergraduate research projects; indeed, it is appropriate that the enrichment provided is monitored and its effectiveness measured (see **section 8.6**). It is necessary that these, as with all research projects, are hypothesis driven. For example, we might suggest that providing food for this tiger up the pole will increase its activity. (Photograph: South Lakes Wild Animal Park)

---

[8] Note that statistical hypotheses, the null hypothesis (H_0) and the alternative hypothesis (H_1), do not fulfil this role because they only predict an effect, and are not related to the underlying scientific rationale of the study.

enrichment, there should be good theoretical reasons for believing that they will achieve their aim and this should be incorporated into the research hypothesis of the study. Otherwise, it will be difficult to be sure that the enrichment is enriching, even if it achieves its planned effect.

Another area in which hypotheses can be difficult to formulate is in the analysis of questionnaires and animal records. Often, the data in these have been collected with no particular question in mind, especially if they are part of routine record keeping. But statistical analysis is only of use if it tests a hypothesis that is derived from theory.

Questions in behavioural research

Research answering any of the four kinds of behavioural 'whys' (see **Box 4.1**) can be undertaken in zoos to find out about the function, causes, development, and evolution of behaviour in particular species. Often, however, the questions are more applied than is the case with wild-living animals and may be concerned with how the zoo environment affects behaviour. It is important to understand that the 'zoo environment' is actually made up of a number of different variables, such as enclosure size, group size, group composition, feeding schedule, and so on, and that each of these may influence behaviour in different ways. Because the scope for manipulating these variables is limited in most zoos, the researcher needs to take particular care in planning a behavioural study in a way that attempts to account for them. Further advice is available in the BIAZA research guidelines (see **Further reading**).

Examples of the sorts of questions that underlie much zoo behavioural research are:

- How does the animal spend its time?
- How does the animal use its enclosure?

In both these cases, the purpose of the question is not usually to have that knowledge for its own sake, but because knowledge of these things can help to answer other questions about how the animal is coping with the zoo environment.

To answer the first question, data are often collected to produce an **activity budget** (**Figs 4.36**

and **4.37**). To collect data for this, the behaviours that the animal performs are collapsed into a small number of mutually exclusive categories, such that each kind of behaviour the animal does can only be scored in one category. Often, these categories are things such as 'resting', 'moving', 'feeding', 'social behaviour', 'sleeping', and 'out of sight', but different categories from these can be used if, for example, the animal has particular behaviours of interest that are hidden within one of these categories. The data collected in this instance are frequencies or durations of behaviour in each category over standardized observation periods, with care being taken to sample all relevant times of the day appropriately. The result shows what proportion of an animal's time is spent in each activity; differences in activity budget between individuals, or between zoos, or between zoos and the wild, can then be examined and, hopefully, interpreted.

To answer the second question—how the animal uses its enclosure—we need to know how often an animal is in each sector of the enclosure. In principle, we would expect all sectors to be used equally relative to their size, but, perhaps surprisingly, many zoo animals do not use all the space available to them. If this is the case, it might indicate that the enclosure is not as well designed for that species as it could be, or that there are things within the cage environs to which the animal is attracted or which it is trying to avoid. But simply knowing how much time the animal spends in each sector is not enough to tell us about its enclosure use. It is likely that the different sectors that we identify are themselves of different area and that even a randomly moving animal will spend more time in a large part of the cage than in a small one (**Fig. 14.11**). Measures of enclosure usage should take this into account (see **Box 14.2**).

14.4.2 Data collection

Again, methods of data collection should, in principle, be no different in zoo-based studies than in those in any other kind of biological research. Thought should be given to the form, amount, and timing of sampling, particularly in studies of
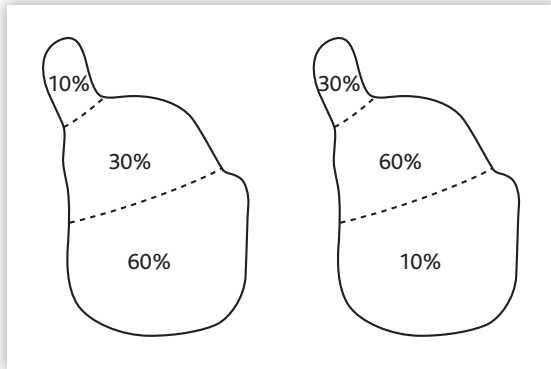
Figure 14.11 The way in which we divide up an enclosure for behavioural sampling may leave us with zones of different areas. We would not be too surprised if an animal spends 10 per cent of its time in the small zone at the top, but if it spends 30 per cent of its time there, we would suggest that perhaps something is attracting it to that zone. Likewise, if it only spends 10 per cent of its time in the large zone at the bottom, we might suspect that there is something there that the animal finds aversive. The SPI helps us to make these sorts of judgements about an animal's enclosure use.

Box 14.2 MEASURES OF ENCLOSURE USE

One measure of enclosure use is the **spread of participation index (SPI)**, which compares the observed frequency of use of different enclosure sectors with the frequency that we would expect, given their relative sizes. The calculated SPI is a number between 0 (indicating all sectors used equally—that is, maximum use of the enclosure) and 1 (indicating only one sector used—hence very great under-usage of available space).

Several investigators have used the SPI to quantify how animals use the space available to them. For example, Traylor-Holzer and Fritz (1985) applied the measure to a group of chimpanzees at a primate centre. They found that adult SPI scores ranged from 0.32 to 0.75, whereas juvenile scores ranged from 0.28 to 0.49, showing greater use of cage space by the juveniles. Shepherdson *et al.* (1993) used the SPI to show increased use of space in a fishing cat *Felis viverrina* on days after live fish had been put in a pool in the enclosure (SPI of 0.4, compared with 0.84 before the arrival of the fish).

As mentioned in the text, the reality of zoo enclosures is that, physically and biologically, they are not made up of equally sized zones, and Plowman (2003) has modified the index to allow for this. Her formula is

$$\text{SPI} = \frac{\Sigma |f_0 - f_e|}{2(N - f_{e\,min})}$$

in which f_0 is the observed number of observations of the animal in a zone (that is, the frequency of its occupation of the zone) and f_e is the expected number of observations for that zone, calculated to account for differently sized zones, but assuming that the animal uses the whole enclosure evenly. N is the total number of observations in all zones, and $f_{e\,min}$ is the expected number of observations for the smallest zone. The resulting SPI is a number somewhere between 0 (greatest use) and 1 (least use).

A similar measure, the **electivity index**, tests for differential usage of different enclosure elements (which could include food sources or enrichment items), rather than just area, but is similar in principle to the SPI. It is calculated as follows:

$$\text{electivity index} = \frac{(W_i - 1/n)}{(W_i + 1/n)}$$

where $W_i = (r_i/p_i)/\Sigma r_i/p_i$, in which r_i is the proportion of time the resource i is used, p_i is the proportion of time it is expected to be used, and n is the number of types of resource (Ross *et al.* 2009). In this case, an electivity index between 0 and 1 indicates over-utilization of a resource (e.g. it may be monopolized by one individual), whereas an electivity index between -1 and 0 indicates under-utilization.

Box 14.3 HOW DO WE SAMPLE BEHAVIOUR?

It is tempting, when studying behaviour, to try to write down everything that every animal does, but it is usually not possible to do this, let alone to derive any meaningful conclusions from what we have written down. Inevitably, we must take samples (**Fig. 14.12**), and this is more of a challenge for behavioural samples than for other type of biological sample (such as faeces, blood, physical measurements), because behaviour changes from moment to moment, but also shows daily and seasonal patterns. We can only give a brief introduction here and anyone wishing to carry out behavioural research is advised to consult more detailed guides, particularly Altmann (1974), Plowman (2006), and Martin and Bateson (2007).

The most detailed data come from 'continuous sampling', in which actual durations and frequencies of individual behaviours are recorded over a fixed period of time. This is usually done to look for all occurrences of a particular behaviour, or to measure the behaviour of each individual animal in turn, or to look for the components of a sequence of behaviours whenever they happen, such as in an interaction. But continuous sampling needs a lot of concentration and can be very time consuming, so many researchers use time sampling instead.

'Time sampling' involves recording the behaviours seen at or between particular points in time (that is, at sample points, or in the sample interval between successive sample points), rather than whenever they occur. This can mean recording the behaviour that occupies more than 50 per cent of the sample interval ('predominant activity sampling'), or behaviours that occupy the whole of the sample interval ('whole interval sampling'). Alternatively, a behaviour can be recorded as present if it occurs at all (regardless of how often or how long) in the sample interval ('one–zero sampling'), or if it occurs at the sample point ('instantaneous sampling' if relating to one animal; 'scan sampling' if relating to several). Time sampling can generate a lot of data rather less intensively than continuous sampling and is particularly suitable for recording long-duration behaviours (that is, 'states', such as sleeping, resting, feeding) rather than those of short duration (that is, 'events', such as biting, pecking, scent marking).

Each of these methods has advantages and disadvantages, depending on what type of data is needed, and how closely the data are required to approximate to real frequencies and durations (Tyler 1979).

Figure 14.12 Behavioural observation requires a sampling methodology. (Photograph: Jeroen Stevens)

behaviour (see **Box 14.3**), and the dependent and independent variables[9] should be defined.

A particular problem with zoo research is that there are quite a few variables present over which the researcher has little control, and these act as confounding variables. This can happen particularly if the data are being obtained from animals in more than one cage, or more than one zoo, but can also cause difficulties in interpreting the results of studies on only one group of animals.

---

[9] The **independent variables** are those that might be manipulated or compared, such as cage size, presence or absence of enrichment, etc., which may change the dependent variable—that is, a behaviour, a physiological measure, or something similar.

How do you know that the effects you are finding are due to the independent variables you are measuring rather than a confounding variable?

As an example, consider how you would investigate whether enclosure size affects behaviour. This would involve getting data from at least two groups of animals, but it is not only in enclosure size that they will differ; they might also have different group sizes and compositions (different numbers of males, females, juveniles, infants, adults), the enclosures may be qualitatively different (moated, glass-fronted, indoor, outdoor, etc.), and the husbandry regimens may be different. So what is the solution?

For small research projects, it is often possible simply to acknowledge that these problems exist, although good experimental design can often minimize them (for example, match the groups as precisely as possible). In larger-scale studies, the multi-zoo approach can allow more independent variables to be measured (see **section 14.6**).

14.4.3 Using other observers

Nowadays it is often the case that a zoo research project might use more than one person to collect data (**Fig. 14.13**). This might be done to save time, to optimize data collection at more than one zoo, or because manpower is available for use. In fact, most personality studies use more than one observer. Observations in the same project are often made by more than one researcher, but recently

Figure 14.13 Many research projects, especially behavioural ones, require more than one researcher collecting data, so it is important to ensure that they are all using the same methods and behavioural definitions. (Photograph: Geoff Hosey)

more researchers have sought to capitalize on keepers, volunteers, and even the public to help collect data. In multi-observer studies it is essential to test statistically that the different researchers are indeed agreed about what the data are that they are collecting, and therefore that their data are equivalent. This is conventionally done by calculating **inter-observer reliability** coefficients, which basically are correlations between two or more data sets collected on the same data. If we apply these to keepers, volunteers and the public, how well do they do? Do they collect usable, publishable data?

The answer, of course, is both 'yes' and 'no'. When two groups of volunteers (high school and university students) were asked to record behaviour and locations of chimpanzees at Johannesburg Zoo, neither group's data agreed with those collected by an experienced observer (Duncan and Pillay 2012), although they were able to provide information about patterns of behaviour. Similarly, visitors to the Wildfowl and Wetlands Trust at Slimbridge, UK, were unable to collect usable data on a group of captive otters, mainly because they exceeded the observation time specified in the instructions (Williams *et al.* 2012). However, these problems are not insurmountable, and certainly with more training volunteers can provide data equivalent to those of researchers.

The same is true for using keepers to collect data. In a study of gorilla inactivity, Less *et al.* (2012) trained keepers at different zoos by video until their inter-observer reliability correlations reached a criterion, and then asked them to collect data. This yielded accurate multi-zoo data in a relatively inexpensive and straightforward way. Of course, keepers often see their animals many times a day, often just in passing. When keepers at Bronx Zoo were asked to note the behaviour of polar bears to enrichment items when they happened to be passing the enclosure, worthwhile data were collected over a five-month period (Canino and Powell 2009).

14.4.4 Practicalities

No matter how well planned a piece of zoo-based research is in terms of its experimental design, it must still take into account several practical
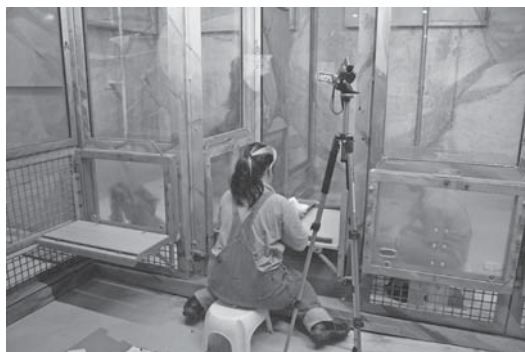
Figure 14.14 Cognitive research requires experimental manipulation through the introduction of various bits of testing apparatus to the animals, as here at Leipzig Zoo. (Photograph: Jeroen Stevens)

issues that make the zoo rather different from other places in which biological research is carried out. Most of these differences stem from the fact that the experimental subjects (usually the animals) are manipulated and influenced in other ways by people (which makes it a little different from the field), but not necessarily by the people who are doing the research (which makes it rather different from the laboratory). Many zoos are understandably unwilling to allow manipulations only for research purposes, but will usually accommodate them if the research is worthwhile, legal,[10] and not too disruptive (**Fig. 14.14**).

By 'manipulations', we mean the sorts of procedure that are often carried out in laboratory research, such as the addition of apparatus to the animals' cages, or changes to cage size or furniture. Such manipulations do take place in zoos, often as part of routine husbandry or enrichment trials, and it is worth the researcher's while building a good relationship with the zoo so that they know when these things are going to happen and can take advantage of the possibilities that they offer.

The perceptions of research held by those zoo personnel who are not directly involved in research are another important factor that must be taken into account during the planning stage of any research project. Sometimes, it is necessary for an animal to be moved (even to a different zoo), or its enclosure is changed, or various other sorts of husbandry changes are introduced during the course of a study, although most zoos will do all they can to avoid disrupting research of which they are aware and in the planning of which they have been involved. It is important that the researcher who wants to work in a zoo establishes a good relationship with the keepers, as well as with the zoo's research department (if it has one), because this can help to minimize these sorts of problems. It is also important for the researcher to realize that whatever they do must be undertaken within the zoo's health and safety procedures (see **Chapter 3**) and ethical guidelines.[11]

One final practical issue is worth mentioning. Much zoo research is undertaken opportunistically, or as a number of small projects by different people at different times, and perhaps using different sampling regimes. If keepers are collecting data, collection often has to fit in with the keepers' schedules of other work, which, again, can be quite challenging for sampling regimes. So how much does this matter when we consider the validity of the data being obtained? Fortunately, the answer is that, in many cases—particularly for the more common behaviours—the answers given by different sampling methods are usually not significantly different from each other (Margulis and Westhus 2008), which means that fitting in with the constraints posed by zoo and university schedules does not mean sacrificing worthwhile data.

[10] The main legislation covering animal research in the UK is the Animals (Scientific Procedures) Act 1986. This is of greater relevance for laboratories and universities than for zoos, but some zoo-based research may require a Home Office licence under the terms of this Act. There is more about this in **section 3.4.4** and **Box 3.4**.

[11] It is important that research is undertaken within the framework of ethical guidelines, and most **accredited zoos** have ethical committees to ensure that all the work of the zoo is conducted ethically. Ethical guidelines for behavioural research are published regularly by the Association for the Study of Animal Behaviour (ASAB) and the Animal Behaviour Society (ABS), and are also available from their websites. There is more information about ethical guidelines for zoos in **Chapter 3**.

14.4.5 Information that is already available

As we have already seen, a lot of data are already available through the record-keeping processes of zoos (**Chapter 5**). Many zoos use the same computerized databases to store their records, and access to these records is possible for approved projects. Other information is stored in **studbooks** and in the International Species Information System (ISIS) database. Investigating these sources of data first is recommended for many research projects, such as those to do with animal health, **demographics**, and genetics.

14.5 Problems in the analysis of data

Most textbooks on data analysis and statistics assume that the research scientist is able to design controlled experiments[12] and have large numbers of subjects. Many of the best-known statistical tests are designed to work with data collected in this way. Thus, parametric tests, which include analysis of variance (ANOVA) for finding differences between conditions and Pearson's correlation r (for detecting association between variables), are widely used in experimental biology, but they require that the data points that they are testing are normally distributed, measured on an interval or ratio scale, independent of each other, and show homogeneity of variance.[13] So what does this imply for zoo research?

Many research studies in zoos gather behavioural data, which may or may not conform to these requirements. But, provided that the data points are independent of each other, non-normally distributed data can still be analysed with non-parametric equivalents of these tests, such as the Kruskal–Wallis test (a non-parametric

equivalent of the ANOVA) and Spearman's test (a non-parametric correlation analysis). What we have to be aware of is the possibility that the data collected in the zoo are not independent, because this renders these tests inappropriate. In many zoo studies, we also have to cope with only a small number of animals (sometimes only one), which again makes these tests unsuitable.

But before we look at how to deal with these problems, let us remind ourselves that the important driver of research is the question that we are asking, or the hypothesis that we are testing. There is nothing intrinsically wrong with having a small number of subjects, or, for that matter, only one; this may well be all that is required to answer the question. So if, for example, we want to find out why a particular animal is performing an abnormal behaviour and how we can reduce it, then issues of sample size are pretty meaningless. Indeed, as Kuhar (2006) has pointed out, inferential statistics have been developed to help the researcher extrapolate from a sample to the population as a whole, but if we are only concerned with our animal and are not trying to say something about other animals in other zoos, then statistical analysis may not be necessary.

It is also worth bearing in mind that non-independence and small sample sizes also occur frequently in field studies of animals, and also in psychology. Provided that they are dealt with appropriately, they need not be a problem. The important thing is that our experimental design and statistical analysis allow for these sorts of issues and give us the answers we need. Ultimately, this might even mean that we break one or two minor statistical rules, which may be better than sacrificing our research, provided that we are honest in our reports of the research and try to discuss whether this affects our conclusions (Kuhar 2006). One way of approaching this dilemma is

---

[12] Control in scientific investigations refers to a group of subjects that do not receive the experimental treatment and therefore show what would have happened had the experimental manipulation not been done.

[13] Homogeneity of variance refers to when the variance of the samples are not significantly different from each other.

to realize that biological significance may sometimes be more important to us than statistical significance. For example, an increase in a stereotypy from 0 to 15 per cent of the time budget of an individual animal is very likely to be biologically significant, but might not be testable statistically because of the zero.

Let us look now at these two problems of non-independence and small sample size.

14.5.1 Lack of independence of data

We think that data are independent if we believe that the value of one data point does not affect the values of any others—but there are three common situations in zoo studies in which this is unlikely to be true: in time sampling, in using animals in the same enclosure, and in constructing activity budgets.

1. *Time sampling* (see **Box 14.3**) This is a convenient way of gathering behavioural data and, if the sample points are close together (that is, at short sample intervals), they allow us to make an estimate of the duration of a bout of behaviour. Short sample intervals also make it more likely that we will not miss behaviours that have a very short duration. Unfortunately, they also risk a problem of autocorrelation.[14] Imagine that you are scoring the behaviour of a red panda *Ailurus fulgens*, which is at the top of a tree asleep (**Fig. 14.15**); if your next sample point is ten seconds later, it is highly likely that the panda will still be asleep at the top of the tree, but even if it is not, there are certain behaviours to which it could not switch in that short time (for example, eating from a food dish on the ground). The best solution is to have sample intervals that are long enough to give you confidence that the animal could, in principle, switch in that time to any of the other behaviours it does. However, this misses most short-duration behaviours, and does not usually allow you to calculate bout durations. But, if these are important,

[14] Autocorrelation means that the value of one sample point is likely to influence the value of the next one.

Figure 14.15 Suppose that you are time sampling this red panda's behaviour: if you sample again in ten seconds' time, what is the panda most likely to be doing? (Photograph: Geoff Hosey)

there are better ways of obtaining them than through time sampling.

2. *Using animals in the same enclosure* Animals in the same enclosure may show the same behaviours at the same time, because they are responding to the same variables (**Fig. 14.16**)—for example, they may all get fed at the same time and they may all receive visitors at the same time—but they also influence each other's behaviours by interacting with one another. Either way, it means that data collected from different animals are not independent. One simple solution is to ensure that samples from the different individuals are taken at different times. If this cannot be done, it may be more realistic to treat the enclosure, rather than the individual animals, as the sampling unit, although this leaves you with a small sample size (see **section 14.5.2**) unless you replicate your study in a lot of zoos. Again, which of these solutions you adopt depends very much upon your research question. For some research projects, it is important to concentrate on individuals and, very often, their social non-independence is exactly what you are interested in—for example, when looking at social interactions in a group of animals.

3. *Constructing activity budgets* (see **Chapter 4**) Activity budgets are very useful as descriptions of how the animal partitions its time between the

Figure 14.16 If you treat each of these animals as an independent subject for behavioural research, how can you be sure that they do not influence each other's behaviour? Is the gerenuk *Litocranius walleri* on the right about to start feeding because the animal next to it is already feeding? (Photograph: Geoff Hosey)

different activities that it does. However, a problem arises if statistical analysis is carried out to compare different activity budgets, because the activities are not independent of each other. Activity budgets, by definition, account for 100 per cent of the animal's time; if the amount of time spent in one activity increases, something else has to decrease to provide that extra time. One solution to this problem is to avoid collecting activity data on all the things that the animal does and, instead, to concentrate on changes in only one or two key behaviours, in which case returning to the experimental question or hypothesis gives an appropriate guide. Alternatively, statistical tests such as the G-test can be used to compare activity budgets (rather than standard parametric and non-parametric ANOVAs), because they do not require independent data categories.

For further information on all aspects of independence problems, including the use of G-tests, see Plowman (2006).

14.5.2 Small sample sizes

Small sample sizes are a frequent occurrence in zoo research. They can occur simply because few animals are available (they may be rare, or big, or live in small groups), or because the effects of a manipulation (such as adding an enrichment) are being studied and the manipulation is only being implemented in one enclosure (maybe even for only one animal).

As pointed out above, this need not in itself be a problem. It can cause some problems of ecological validity[15] if you are trying to extrapolate to the whole population or taxon, but much zoo research is about the particular, rather than the general. It can also cause some statistical problems when you analyse the data. With small sample sizes (that is, a small *N*), it is usually not possible to tell whether or not the samples satisfy

---

[15] Ecological validity relates to how well results from a sample can be generalized to the population as a whole.

the assumptions of the test (such as normality of distribution, homogeneity of variance), but, in any case, the low N may give the statistical test low power. This means that the test is unlikely to detect meaningful differences unless the pattern of the data is very strong indeed.

A reasonable rule of thumb is that if there are eight or more individuals in each of the groups being compared, standard parametric and non-parametric tests should work reasonably well. With a smaller N than that, the best solution is to analyse the data with randomization tests[16] instead (Besag and Clifford 1989; Manly 1998; Todman and Dugard 2001).[17] What must be avoided is simply gathering more data on the same animals in the hope that these extra data points increase the sample size; they do not, because you should be using only one mean or median for each animal, or else using separate data points in a repeated measure design. This fault is known as pseudo-replication,[18] and is discussed more fully by Kuhar (2006).

Randomization tests are designed to identify the probability of finding a particular pattern of scores across two or more groups. Suppose, for example, that you are investigating whether activity increases in an animal that is given a feeding enrichment and, to answer this question, you collect baseline (that is, pre-enrichment) activity data for 20 days and treatment (that is, with enrichment) activity data for a further 20 days. The randomization test then asks into how many different combinations can the resulting forty numbers (that is, the twenty baseline data points and the twenty treatment data points) be put and, out of all of these, what is the probability of getting low values in the baseline group and high values in the treatment group. This test makes no assumptions about the underlying distribution of the data, but it does require that the experimental design includes some randomization. This can be achieved by randomly allocating the treatment among the available observation blocks.

More information on randomization tests in the zoo context is given in Plowman (2006).

14.6 Multi-zoo studies

Many of the research questions that we are interested in asking about zoo animals cannot be answered from single-zoo studies, but require data drawn from a number of different zoos (Melfi and Hosey 2012). Multi-zoo studies of this sort allow much more than a possibility of increasing sample size; they also allow us to start teasing out the effects of a number of different variables, which would remain confounding variables if we were to restrict ourselves to only one zoo. Furthermore, multi-zoo studies are the only real way of finding out about the prevalence of phenomena in which we are interested (such as how widespread is a particular behaviour, a particular parasite infestation, or a particular dietary anomaly), or to confirm whether or not something appearing in our zoo is unusual.

There are, of course, some limitations to multi-zoo research as well. Because zoos are so different, you may end up actually introducing even more confounding variables into the study. There is also the risk that pooling data from animals in different zoos can lead again to lack of independence (Kuhar 2006), because animals in the same cage have more in common with each other than they do with animals in different cages or different zoos. There may be practical (and financial) difficulties inherent in visiting a number of zoos, possibly in different parts of the world. Finally,

---

[16] Also called permutation tests, randomization tests calculate a test statistic and compare it with the results from repeated randomization of the same data across all groups. This identifies the probability of obtaining a particular pattern of scores when all the possible combinations of scores are jumbled up.

[17] Todman and Dugard's (2001) book on randomization tests comes with a useful CD with worked examples of how to carry out these tests.

[18] Pseudo-replication is the term usually used to describe data among which the sample points are not independent. For example, fifty measurements of stride length by a cheetah do not give you a sample size of 50; the sample size (n) is 1 (the cheetah).

gaining the cooperation of a lot of different zoos is much more of a challenge than working only in your local zoo, and can be both time-consuming and frustrating. This process can, of course, be eased considerably if the project is supported by the relevant zoo association; for example, in the UK and Ireland BIAZA will scrutinize and support, through its Research Group, multi-zoo projects that have achievable and worthwhile goals (see **Box 14.6**).

There are several ways in which multi-zoo research can be undertaken. Often, they involve a survey of some sort, usually using a questionnaire, and may request current information or historical records. Surveys are widely used to investigate husbandry problems, but are often not used to best advantage because of poor design (Mellen 1994). However, when carried out well, they can supply much useful data very quickly. A good example of this approach is seen in a survey by Pickering *et al.* (1992) to determine what factors affect the breeding success of captive flamingos (see **Box 4.3**). They obtained information from forty-four zoos in the UK and Ireland on flock size, egg-laying, and chick-rearing in Chilean *Phoenicopterus chilensis* and Caribbean flamingos *P. ruber ruber*. They found that larger flocks were more likely to breed successfully, and recommended minimum flock sizes of forty birds (Chilean) and twenty birds (Caribbean) to ensure breeding, provided that space allowed these numbers without crowding.

Another way of undertaking a multi-zoo study is to visit each zoo and collect data in person. This is usually the only way of conducting behavioural studies, because quantitative behavioural data are not routinely gathered by zoos and hence none would be available for a survey- or questionnaire-based approach.

An example is the study by Perkins (1992) of the factors that affect activity in orang-utans *Pongo pygmaeus* (**Fig. 14.17**). She observed twenty-nine animals in fourteen enclosures across nine different zoos in the USA, and then used multiple

Figure 14.17 Behavioural observations of orang-utans in many different zoos, referred to as 'multi-zoo studies', have shown that they prefer large enclosures with a lot of movable objects and opportunities for social interaction. (Photograph: Ray Wiltshire)

regression[19] to identify the effects of the different environmental variables that she measured. This allowed her to conclude that large enclosures with a lot of movable objects, together with opportunities for social interaction, were the most favourable environments for promoting activity in these animals. To many people, a result such as this may seem self-evident, but in fact it is not; it may tell us something that we think we already know, but we actually do not know it at all unless it is supported by hard empirical data and, in this case, using data from a number of zoos allowed these data to be collected in a way that would not usually be possible in a single zoo.

To show just how much a multi-zoo study can achieve, let us look finally at a study by Carlstead *et al.* (1999a; 1999b) on black rhinoceros *Diceros bicornis* (**Fig. 14.18**) in US zoos. This was part of the Methods of Behavioral Assessment (MBA)

[19] Multiple regression is a statistical technique for identifying which of a number of independent variables best predicts the value of a dependent variable—in this example, activity.

Figure 14.18 The black rhinoceros *Diceros bicornis* was the subject of a US multi-zoo study that aimed to identify the reasons for the species' poor reproduction in captivity. (Photograph: Ray Wiltshire)

project, originally set up by researchers from twelve leading US zoos and designed to assess the behaviour and breeding success of animals across a large number of zoos. In this way, standardized behavioural profiles could be built up and compared across zoos to identify the influence of both individual differences (that is, 'personality'—see **Box 4.2**) and captive management regime on breeding success, mortality, behaviour, and welfare. The black rhinoceros was one of the species chosen for this study because it reproduces poorly in captivity. Such a study would not be possible in only one zoo and a survey would not give all the information that was required. A multi-zoo study using breeding records, keeper assessments of animal traits, enclosure measurements, and behaviours allowed this study to conclude that the most compatible rhinoceros pairs were those with assertive females and submissive males, and that they bred best in large enclosures with few

concrete walls. Such conclusions could only be drawn because the multi-zoo study allowed the comparison of almost thirty pairs of rhinoceros.

14.7 Disseminating the results of zoo research

It should be clear by now that good zoo research should address a particular question or hypothesis, should collect relevant data through appropriate methods, and analyse those data in such a way as to provide an answer to the research question. All that then remains is to make that research available to other people (see **Box 14.5**). No matter how good the research may be, it is of greatest value if it is made available to other people. In the case of zoo research, this means making it available not only to other zoo professionals, but also to researchers in other fields and to anyone else who may find it useful or interesting. So how is this done?

The most important way is through publication in peer-reviewed journals[20] and there are a number of these that publish zoo research. The advantages of this are that, by being published in these journals, the research has been shown to be of good quality; furthermore, this sort of publication ensures that the results of the research are available to anyone who wishes to see it. By their very nature, however, peer-reviewed journals tend to be mostly concerned with studies that have high ecological validity, which rather restricts the opportunities for much of the zoo work to be acceptable to them. Consequently, a lot of zoo research is published in the so-called 'grey literature'—that is, journals that are not peer-reviewed and which are often zoo community periodicals or internal publications of individual zoos (see **Box 14.5**). This makes the research available to others within the zoo community, but getting access to these sources can be difficult for those outside this community. This difficulty is recognized by

---

[20] **Peer-reviewed journals** are those that publish papers only once they have been through a rigorous evaluation by independent experts to ensure their quality and scientific value.

Box 14.4 CASE STUDY: A COMPLETED RESEARCH PROJECT

Let us look at an example of a piece of zoo research which has been through all the stages identified in this chapter. The research concerned a 13-year-old female olive baboon *Papio hamadryas anubis*, who showed self-injurious behaviour (SIB) (see **section 4.4.1**), notably biting her arms and legs and pulling out hair from her head and arms. One of the hypotheses, derived from the literature on SIB, which could account for this behaviour was that it was accidently being reinforced by the animal's caregivers, for example by paying her more attention when she performed SIB, or by allowing her to avoid unpleasant events happening at those times. If this turned out to be the case, then the possibility was raised of her learning different consequences by reinforcing different behaviours instead.

The study involved several observers, who used an ethogram (see **section 4.1.1**), and whose inter-observer reliability was calculated (over 90 per cent agreement for each behaviour). Several experimental treatments were then applied (such as ignoring the SIB, paying attention to it but reprimanding the animal, or differentially reinforcing a different behaviour (lip-smacking). It was found that the mean percentage duration of SIB was 23 per cent in the attention condition, but only 2.5 per cent in the ignore condition, thus supporting the hypothesis that the SIB was being reinforced by caregivers. During treatment the lip-smacking gradually increased and SIB decreased through differential reinforcement. Finally, the researchers published their study in a peer-reviewed journal (Dorey *et al*. 2009).

Box 14.5 ZOO JOURNALS

One of the earliest zoo-related journals was *Zoologica*, published by the New York Zoological Society from 1907 to 1973 (Kisling 2001), but now no longer published. In the UK, the Zoological Society of London has been publishing the *International Zoo Yearbook* annually since 1960. The journal *Zoo Biology* was first published in 1982 and remains the main peer-reviewed journal for zoo research. At the time of writing (October 2012) a new EAZA-sponsored open-access web-based journal, the *Journal of Zoo and Aquarium Research*, is imminently due to be launched. In Europe, the journal *Der Zoologische Garten* publishes papers on zoo animal management, mostly in German. Several journals routinely publish the results of research on zoo animals—notably, *Animal Welfare*, *Applied Animal Behaviour Science*, and the *International Journal of Primatology*. Veterinary and health-related research on zoo animals is published in a number of journals, such as *Journal of Zoo and Wildlife Medicine*, *Journal of the American Veterinary Medical Association*, *Journal of Parasitology*, and *Journal of Veterinary Medical Science*.

The magazine *International Zoo News* is not a peer-reviewed journal, but has the advantage of being readily accessible; this publication makes many of its articles and back issues freely available online. Other zoo news, particularly relating to conservation, is published in *Dodo*, the journal of the Jersey Wildlife Preservation Trust, but this is harder to come by, because this publication does not have its own website.

Zoo associations have, of course, published their own newsletters from the outset. Some of the more notable of these include the AZA's *Communiqué* and the American Association of Zoo Veterinarians (AAZV) *Journal of Zoo Animal Medicine*. Within Europe, BIAZA and EAZA both produce their own newsletters (*Lifelines* and *Zooquaria* respectively). The BIAZA Research Group also publishes regular summaries of zoo research news, available online from the BIAZA website.

Zookeepers also have their own journals and magazines: the Association of British Zoo and Wild Animal Keepers (ABWAK), for example, produces *Ratel*, and the Australasian Society of Zookeeping produces *Thylacinus*. Finally, there are journals such as *Shape of Enrichment* which report new ideas and advances in husbandry. These magazines and newsletters, often referred to as the 'grey literature' because the articles in them are not peer-reviewed, are nevertheless a useful source of additional information on zoo research and other activities.

> ## Box 14.6 MANAGING AND COORDINATING ZOO RESEARCH
>
> Research in zoos can be achieved on an individual basis, but is much more effective if it is part of a coordinated effort. Coordination helps avoid duplication of effort, allows better integration of knowledge from different sources, and can help to ease some of the logistical difficulties involved in implementing research.
>
> In the UK and Ireland, BIAZA takes on this coordinating role through its research group. This group publishes a regular newsletter, giving information on current projects, and organizes an annual zoo research symposium, the proceedings of which are published by BIAZA and made available on the BIAZA website. It also lends support to approved projects (which can help to increase response rates in multi-zoo surveys) and publishes a series of guidelines to help researchers in various aspects of zoo research.
>
> Research is also supported by EAZA, which endorses two research meetings that are held in alternate years at Poznan Zoo in Poland and by the Leibniz-Institut für Zoo- und Wildtierforschung (Leibniz Institute for Zoo and Wildlife Research (IZW)) in Berlin, respectively. The IZW studies
>
> behaviour, evolutionary biology, wildlife diseases, and reproduction in both wild and zoo animals. EAZA and the IZW publish research and hold regular conferences on zoo and wildlife research. EAZA is currently preparing a research strategy, which will place a strong emphasis on **taxon advisory groups (TAGs)** to develop research themes and keep records of research on their species. This means that, in future, one of the first things that a researcher should do is contact the relevant TAG for the species in which they are interested to find out who else is undertaking research on it.
>
> In North America, the AZA includes research in its annual and regional conferences. Proceedings of these are published, and the most recent ones (since 2004) are available on the AZA website. AZA also maintains a searchable database of research projects although, unfortunately, this is only available to AZA members.
>
> Nevertheless, much zoo research is still based in individual zoos, and there is a good case to be made that more prioritization of research across zoos would be beneficial (Hutchins and Thompson 2008).

the WZACS (WAZA 2005), which urges zoos to publish in the peer-reviewed literature wherever possible.

Ultimately, the research should be published in the most appropriate place, bearing in mind the intended readership. BIAZA has produced guidelines on getting zoo research published; these include a list of suggested journals (Pankhurst *et al.* 2008).

Much zoo research is presented and discussed at conferences. Regular research conferences are run by BIAZA, EAZA, AZA, and other zoo associations, as well as by organizations such as the Leibniz Institute for Zoo and Wildlife Research (IZW) (see **Box 14.6**), and details of these are usually available at their respective websites. Conferences are a good way of disseminating research findings, because they make the material available for discussion

and draw people's attention to research of which they may otherwise be unaware.

14.8 What zoo research still needs to be done?

Let us finish off this chapter by briefly considering some areas of zoo biology in which research still needs to be done. You will have noticed in several chapters that we have said things such as 'very little is known about …', so, in this section, we will try to recall some of these as a kind of summary of where we think future research should be directed.

We can start with two general, but very important, priorities. Firstly, more zoo research needs to have a more explicit conservation focus. This is, in any case, a legal requirement now for zoos in many European countries, including the UK

(see **sections 3.1** and **10.3**), although, as we have seen, there have been some criticisms of how effective this legislation is. How can this be done? One obvious way is to undertake research on the *ex situ* population, which can then feed back to, and inform, the management of the *in situ* population. One area in which zoos have great expertise already is in the management of small fragmented populations (Wharton 2007).

Secondly, much more research should be done on non-mammalian species. In putting this book together, we have often struggled to find suitable examples among the invertebrates, fish, reptiles, amphibians, and even birds, in a literature that is very much dominated by mammalian examples.

The following list represents some areas of zoo biology in which we think that there is scope for worthwhile research projects. The list is mostly the same as the one we put in the first edition of this book, which perhaps emphasizes that after four years all of these still need doing!

- How does tagging, microchipping, or branding of animals affect their behaviour, physiology, and welfare? This has relevance for the study of wild animals, as well as animals in the zoo.

- Do animals in zoos learn about husbandry events and how does this manifest itself?

- How does seasonality in northern zoos influence the behaviour and physiology of tropical animals?

- What are different animals' preferences and **responses** to different physical **stimuli** in their environment, such as sound (including **ultrasound**), light, humidity, and temperature?

- What do different species require in their housing, in terms of privacy, elevated areas, etc.?

- Is space quality more important than quantity? (The current evidence is almost all from primates.)

- How does the timing of feeding and the way in which the food is presented affect the animals?

- How do differences in group composition and group size affect the behaviour and welfare of the animals?

- How do different species interact with one another in **mixed-species exhibits**?

- How do animals respond to changes in their housing?

- What behaviours do fish, reptiles, and amphibians show that are equivalent to those abnormal behaviours (such as stereotypies) that are sometimes seen in birds and mammals?

- Can **preference testing** be achieved with zoo animals to give us information about their welfare?

- How do non-mammalian species respond to the presence of zoo visitors?

- What are the optimal housing conditions for captive breeding across a range of endangered species?

- What can an analysis of zoo records tell us about **life history traits**, such as tooth eruption patterns, length of gestation, and litter size, in various species?

- Cognitive welfare indices.

- Effects of presentations and the use of animals in shows.

- Is zoo education effective?

Finally, it is worth pointing out again that zoos are excellent places in which to research the basic biology of species that would be difficult to study in the wild and about which little is known—and there are a lot of those.

To illustrate this, in the first edition of this book we named five species that had either had their conservation status reclassified or had appeared for the first time in the 2007 IUCN Red List, and looked to see how many times they had appeared in the title of a scientific paper in the ten years between 1998 and 2008. Here are those same five species with, additionally, the number of times they have appeared in a paper title between 2009 and 2012:

- western lowland gorilla *Gorilla gorilla gorilla* (1998–2008: 537 times; 2009–2012: 185 times);

- Malayan sun bear *Helarctos malayanus* (1998–2008: 23 times; 2009–2012: 11 times) (**Fig. 14.19**);
- Rüppell's griffon vulture *Gyps rueppelli* (1998–2008: not at all; 2009–2012: once);
- gharial *Gavialis gangeticus* (1998–2008: five times; 2009–2012: three times);
- Banggai cardinal fish *Pterapogon kauderni* (1998–2008: 26 times; 2009–2012: not at all).

The clear message is that the vulture, the gharial, and the cardinal fish still really need studying. And there are thousands more species, too, many of which are there waiting for study at a zoo near you.

Figure 14.19 The Malayan sun bear *Helarctos malayanus*, one of many species that has not been studied as much as it should. (Photograph: Geoff Hosey)

Summary

- Research in zoos can be designed to answer applied questions about the maintenance of animals in captivity, or can answer basic questions about the biology of the animals.
- Zoo research is growing in quantity, but is still biased towards both particular topics (behaviour, reproduction) and certain taxa (carnivorous mammals, primates, and others).
- Increasingly, zoo research is undertaken by research departments or individual researchers within zoos.
- Experimental designs in zoo research usually have to contend with difficulties caused by small sample sizes and non-independence of data, but this not problematic for all questions or hypotheses posed.
- Multi-zoo studies can avoid some of these problems and can also answer research questions that could not be answered in single-zoo studies.
- The results of zoo research are published in journals and discussed at conferences, but more needs to be done to make data more accessible.

Questions and topics for further discussion

1. What difficulties of sampling and analysis might you encounter in a research project on zoo animal behaviour?
2. What do you think are neglected areas of zoo research and why?
3. Provide an argument that worthwhile behavioural studies can be undertaken in zoos.
4. What are the advantages and disadvantages of multi-zoo research?
5. 'Small numbers of animals need not be a problem in zoo research.' Discuss this assertion.

Further reading

A good overview of trends, opportunities and challenges in zoo research is provided by Maple and Bashaw (2010); the focus of their discussion is the AZA area, but most of what they say is of relevance elsewhere in the zoo community as well. General principles of biological research are covered in Barnard *et al.*'s *Asking Questions in Biology:*

Design, Analysis and Presentation in Practical Work (1993). Anyone interested in undertaking behavioural research in a zoo should consult a good manual, such as Martin and Bateson's *Measuring Behaviour: An Introductory Guide* (2007), or Lehner's *Handbook of Ethological Methods* (1998), or Ruxton and Colegrave's *Experimental Design for the Life Sciences* (2010) before they start.

For a discussion of some of the statistical challenges in zoo research, we recommend Kuhar (2006). For a more general guide to statistics, a very user-friendly textbook for undergraduates is Hawkins's *Biomeasurement: A student's Guide to Biological Statistics* (2009), The underlying concepts and the practicalities of zoo research are well covered by the series of *Zoo Research Guidelines* published by BIAZA and available for free download on the BIAZA website. This ongoing series currently covers:

- project planning and behavioural observations (Wehnelt *et al*. 2003);
- statistics for typical zoo data sets (Plowman 2006);
- monitoring stress (Smith 2004);
- effects of human visitors (Mitchell and Hosey 2005);
- questionnaire design (Plowman *et al*. 2006);
- behavioural profiling (Pankhurst and Knight 2008);

- how to get zoo research published (Pankhurst *et al*. 2008).
- aquarium research (Hill and Sharpe 2010);
- multi-zoo research (Melfi and Hosey 2012);
- nutrition and diet evaluation (Fidgett and Plowman 2009).

Websites and other resources

Methods of implementing zoo research are described in the various research guidelines published by BIAZA and listed above, all of which are available online at **http://www.biaza.org.uk**. Copies of BIAZA Research Conference Proceedings and the regular research newsletters can also be obtained from this site.

Anyone interested in undertaking behavioural research in a zoo should investigate the zoo website for information about what sort of research it might be possible to undertake there and what special application procedures may apply, because they will need to request permission to conduct their research there first.

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.
http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Chapter 15
We hope you enjoyed your visit

In much the same way as many zoos have a sign near the exit saying 'We hope you enjoyed your visit', we hope that you have enjoyed reading this book and have found it useful. Our aim in writing this book was to provide a greater awareness of what zoos do, of the different points of view within and about the zoo profession, and of the many and complex issues modern zoos must deal with if they are to continue to operate. The perspective we have adopted has been that increasingly the operation of zoos and management of animals needs to be evidence-based, and we have given a explanation of what that means (see **Box 6.3**), as well as illustrating this approach through the examples we have given in each chapter.

Although all of us have worked in or been involved with zoos for many years, we are not, we hope, blindly uncritical of the zoo profession. There is much that zoos could, and should, do better, and we have tried to address this in the previous chapters. We would be among the first to acknowledge that there are some poor zoos, in which standards of husbandry and welfare are not as high as they should be, and in which the contribution of the zoo to conservation, or education, or research, is minimal. But we believe that the community of **accredited zoos** worldwide takes very seriously its responsibility for raising standards and for providing support to fellow members—and indeed for zoos that are not yet members of a national or regional accrediting body (see **Section 15.5.3**)—to continue to become better at what they do.

In this final chapter, we want to revisit some of the themes that we introduced at the start of this book and to consider how well zoos match up to what they say about themselves in their mission statements (**Fig. 15.1**). We saw, in **Chapter 1**, that zoos tend to describe their role in terms of four Keywords: conservation, education, research, and recreation. But how good are zoos at measuring their success in achieving their stated objectives, and to what extent do zoos critically evaluate their impact in areas such as conservation, education, and research? And how will this sort of evaluation affect the kinds of animals we see in zoos and the way in which these animals are managed? We also want to return to the subject of **sustainability**, which we have touched on only briefly in earlier chapters. For those readers who are interested in finding a job in a zoo (or who want to develop further an existing zoo career), we have provided a short section on some of the training and career opportunities within the zoo profession. Finally, we end this chapter by taking a look at some of the more challenging or controversial issues facing zoos today.

Therefore the structure of this short concluding chapter is as follows.

15.1 **Evaluation**
15.2 **The shape of the collection**
15.3 **Sustainability**
15.4 **Careers in zoos**
15.5 **Challenges for the future**

Figure 15.1 How well do zoos match up to their mission statements? Zoo and aquarium mission statements often mention conservation and education as key roles, and many zoos provide opportunities for hands-on contact with animals as part of their educational programmes. This might include touchpools, shown here as part of an educational display. (Photograph: Jeroen Stevens)

15.1 Evaluation

The evidence-based approach to zoo science extends beyond providing a basis for animal management, and also provides the evidence for the other activities that zoos are involved with. Zoos have, of course, been evaluating their contributions to conservation (see **sections 10.3.5** and **10.6**), education (see **section 13.2**), and research (see **section 14.3**) for some time. In recent years, for example, studies such as those of Conway (2003), Miller *et al.* (2004), Balmford *et al.* (2007), and Mace *et al.* (2007) have assessed the achievements of zoos and aquariums in achieving conservation and education goals. Prompted at least in part by these studies, zoos are becoming better at self-evaluation and at recognizing the need to measure achievement against clear objectives. For example, two of the four main recommendations to emerge from the Fourth International Conference on Environmental Education (ICEE)[1]

(ICEE 2007) were about how zoos should set and utilize appropriate benchmarks, and then evaluate their performance against these benchmarks. The European Association of Zoos and Aquaria (EAZA) Education Standards (EAZA 2008) now explicitly require member zoos to evaluate the effectiveness of their educational programmes.

Accredited zoos are also often required by their national or regional zoo association to undertake a process of self-evaluation. To take just one association, the Canadian Association of Zoos and Aquariums (CAZA) requires its member collections '*To establish, maintain and raise standards of operation in the Canadian zoo and aquarium community through a process of self-evaluation, on-site inspections and peer review*'. Conservation strategy documents produced by zoos, such as the report from the international amphibian *ex situ* workshop held in Panama in 2006 (Zippel *et al.* 2006), now include both detailed action plans and a requirement to

---

[1] Confusingly, ICEE is the acronym for more than one organization. Within the zoo world, ICEE is usually a reference to either the International Conference on Environmental Education, or the International Conference on Environmental Enrichment. The former is a major intergovernmental conference sponsored by UNESCO and UNEP; these meetings are held once each decade (the first was in Tblisi, Georgia, in 1977). The latter is a conference focused on enrichment and animal welfare, held every two years (with the first in 1993).

evaluate achievement of the stated objectives in these plans. Taronga Zoo in Sydney refers to achieving '*tangible conservation outcomes*' in its mission statement; implicit in this is the measurement of the effectiveness of the zoo's activities to support wildlife conservation.

There is, of course, a risk that zoos may evaluate the wrong things. It is tempting—and perhaps easier—to measure and report on inputs (funds raised, money spent, number of people employed) rather than to assess impact, or outputs (number of threatened species in captive breeding programmes, successful reintroductions back into the wild, etc.) (see Mace *et al.* 2007; Kapos *et al.* 2009). The zoo community is not unaware of this risk. During the run-up to the 2004 *Catalysts for Conservation* symposium, for example, zoo professionals collaborated with leading conservation biologists in an independent research group, the Zoo Measures Group, to facilitate the process of measuring the success of zoo conservation initiatives (Leader-Williams *et al.* 2007). The findings of this group were used in the preparation of some of the papers reported at the symposium and subsequently incorporated into various chapters of the book *Zoos in the 21st Century: Catalysts for Conservation?* (Zimmerman *et al.* 2007). More recently, WAZA and Chester Zoo have taken the methodology outlined by the Zoo Measures Group a step further, and have developed the WAZA Project Conservation Impact Summary Form (available online at **http://www.waza.org/en/site/conservation/conservation-impact**). As the WAZA website states, the form '*is designed to provide an easy format for project coordinators to summarise project achievements and for these achievements to be evaluated for their conservation impact*' (WAZA 2012). A greater emphasis on this sort of project evaluation is likely to lead to changes in the shape of zoo collections in the twenty-first century, and this is the subject of the next section.

This sort of evaluation includes the fourth of the main roles of zoos, that of recreation, by providing a good day out (**Fig. 15.2**). 'Gate income' is a very effective indicator of whether or not a zoo
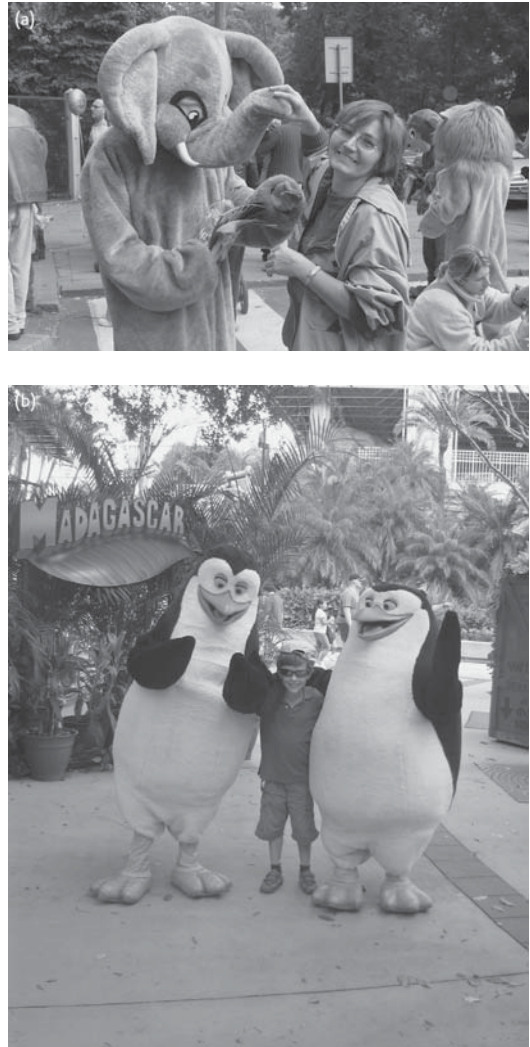
Figure 15.2 There is nothing wrong with zoos emphasizing a good day out in their marketing material, if this allows them to get across other messages about threatened species and conservation after people arrive. (Photographs: (a) Warsaw Zoo; (b) Sheila Pankhurst)

is providing what visitors want. There is nothing inherently wrong with zoos wanting their visitors to have a good day out, particularly if this also helps the zoo to get across other messages about conservation or animal welfare. But more extensive and detailed evaluation can provide important, and sometimes surprising, insights into what visitors do, and what they want to do, during their zoo visit. For instance, Taronga Zoo in Sydney undertook a tracking study of visitors

between 2009 and 2010, which showed, amongst other things, that the zoo might benefit from slowing the visitors down, providing more (and more active) experiences and better facilities (Taronga Conservation Society Australia/VisionXS, unpublished). After various initiatives were introduced as a result of this study, a follow-up study in 2012 showed an increase in average stay length (from 3.5 to 4.25 hours) and a decrease in the average number of experiences per hour (from 9.24 to 7.49). Interestingly, the attraction which received the most visits was Reptile World (which had an average visit time nearly five times longer than gorilla outside viewing), but the spider show (**Fig. 15.3**), which attracted many fewer visitors, had the longest stay times for those who did attend. Data like these are important because they challenge many of our preconceptions about what visitors want to see.

Zoos, of course, rely heavily on their visitors to provide income, not only to meet their day-to-day running costs, but also for supporting their conservation work, both *ex situ* and *in situ.* There is a danger that too great a pressure on zoos to focus on conservation, education, and research, with recreation seen as the poor cousin and rather frowned upon as a worthwhile objective in its own right, will result in zoos that are worthy, but dull, and which no one wants to

Figure 15.3 Many people profess to dislike spiders, like this red-kneed tarantula *Brachypelma smithi,* but visitor stay times at spider shows can be quite long (Photograph: Jessica Goldman)

visit. There is even a danger that the World Zoo and Aquarium Conservation Strategy (WZACS) (WAZA 2005) may direct attention away from other worthwhile areas of activity and research by zoos, such as welfare and **enrichment**. And, as the current President of BIAZA, Sir Drummond Bone, has pointed out in a conference talk, people are unlikely to learn anything in zoos if they do not enjoy the experience. His view is that recreation '*should not be a dirty word*' if zoos are to achieve their goal of educating visitors about wildlife conservation.

Looking at the wider role of zoos in modern society, an initiative by nine UK zoos, in partnership with the British and Irish Association of Zoos and Aquariums (BIAZA), resulted in the production of *The Manifesto for Zoos* (Regan 2005). This was an ambitious attempt to evaluate not only zoo performance in the field of conservation, but also to assess how zoos can and do contribute to a wider 'public good'. The *Manifesto for Zoos* has sections covering, for example, the economic output of zoos, and zoos as vehicles for local and regional regeneration. More recently, EAZA has undertaken a survey of the socio-economic impact of its members on the European economy (Kim *et al.* 2010). This showed that EAZA members generated €2,461 million of added value in the European economy, made up from both on-site and off-site spending, and employed 31,600 people directly and helped to create a further 11,300 jobs indirectly in the wider community. Surveys such as these demonstrate the importance of the zoo profession not only in achieving conservation and education goals, important though these are, but also as active and productive agencies within the wider community.

15.2 The shape of the collection

As with a visit to a zoo, you might not have found everything you expected to see, or wanted to find out about, in this book. Of course, we hope that the opposite is also true, and that you have found some things in the last fourteen chapters that,
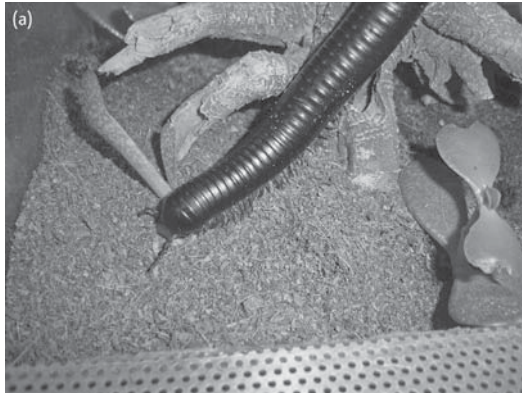
Figure 15.4 There is a perception that zoos are largely about mammals and birds, although, in terms of the total number of species held in zoos and aquariums, other taxa, especially (a) invertebrates like this millipede *Archispirostreptus gigas* and (b) fish, are often well represented. (Photographs: (a) Mathias Mende; (b) Warsaw Zoo)

perhaps, you did not expect to find, but which you found interesting.

We have seen in this book that there is a bias in zoo collections towards mammals and birds (although, in terms of the total number of different species, invertebrates do quite well, particularly if corals and other marine animals are included). One consequence of this is that there are more examples of studies on mammals and birds in this book than there are on reptiles, amphibians, fish, and certainly invertebrates (**Fig. 15.4**). The zoo world is changing, however, and in some areas it is changing quite rapidly. Zoos are keeping more threatened species. The number of non-mammalian species managed as part of coordinated **captive management programmes** is now greater than surveys from the 1990s suggested, although **taxa** such as amphibians, fish, and invertebrates are still under-represented (Conde *et al.* 2011). But the success of aquariums such as The Deep in Hull, UK,[2] shows that visitors will come in large numbers to see fish and other marine animals (**Fig. 15.5**), and demonstrates that the zoo bias towards mammals and birds is not necessarily reflected in what the public is prepared to pay to see. Balmford *et al.* (1996),

in a series of censuses of visitors at London Zoo, found that the aquarium and the reptile house were among the most popular exhibits, which is concordant with the Taronga tracking study we mentioned in the previous section. This also fits with suggestions that zoos should concentrate on smaller species (see **section 10.7**), and zoos take very seriously the issue of collection planning, and which species should be prioritized (see **section 9.7**). So what will we see in zoos in future years? Probably many of the animals we see there

Figure 15.5 Aquariums are very popular, particularly where walk-through tunnels offer such good viewing of aquatic animals. (Photograph: Jeroen Stevens)

[2] When The Deep opened in 2002, the aquarium predicted visitor numbers of 200,000 in its first year. In fact, more than 500,000 visitors came to The Deep in the first five months (Garner 2002).

Box 15.1 SOME PREDICTIONS FOR THE FUTURE

What are the other changes that we are likely to see in zoos over the coming years? In terms of the visitor experience, at least fifteen EAZA zoos now have hotels on site and this looks likely to become a future trend. Families visiting theme parks or leisure complexes often stay for a weekend, or longer—why not at zoos? The zoo of the future may well have, alongside its animal collection, a separate natural history discovery centre, or perhaps an IMAX[3] cinema showing the best of wildlife films.

Here are some of the ideas that were discussed at a 2012 symposium in the USA, entitled '*The Future of Zoos*', which was attended by many of the leading figures from and associated with the zoo world (The talks given at this symposium can be viewed online, at **http://www.canisiusishar. org/symposia/future_of_zoos.htm**).

One prediction was that zoos will become larger, and the distinction between zoos and wildlife parks or reserves will blur. Already the boundaries of national parks in parts of Africa and elsewhere are increasingly being fenced, and so the wild animals in these areas are not completely free to roam (Conway 2003). Other contributors to the symposium emphasized research, and saw the emergence of zoo–museum hybrids with a strong emphasis on scientific research in support of conservation. This harks back, in many ways, to the era of the Jardin des Plantes and the creation of London Zoo, which we looked at in **Chapter 2**.

The symposium also looked at developments in technology which would allow the zoos of the future to consider cloning currently extinct animals, such as the cave bear, the woolly mammoth, or the thylacine; but also pointed out that creating the impression that conservation mistakes (such as extinctions) can be reversed by the use of techniques such as cloning is potentially dangerous and could undermine wider conservation initiatives. Michael Noonan (Canisius College Institute) predicted rapid future growth in robotics and computer 'wetware' in zoos—it is well worth watching the video clips in his talk, showing the current generation of robotic animals, such as 'Big Dog' (see **http://www.canisiusishar. org/symposia/future_of_zoos.htm**), and imagining what a robotic tiger could look like in 50 year's time.

But perhaps the last word from the symposium should go to Bill Conway, and should be about the role that zoos can play in wildlife conservation. Conway said:

> 'The next few decades may be our last chance to save much of the Earth's most wonderful wildlife. Only a little bit of this can be done directly by zoos, but much can be done with the help of zoos...... as they evolve to become field-based nature conservation organisations... Zoos are, after all, the only institutions our society has ever created for the exhibition and care of wildlife. It is a paradox that they have not yet made conservation of wildlife their highest priority. Their future is to do so.'

now, as commitment to sustainable groups is very much a long-term endeavour. Perhaps we will see more small species. Some of these may be very small! For example, Artis Zoo, in Amsterdam, is developing a major new exhibit dedicated to

microscopic life forms. The MicroZoo will be part of a new Knowledge Square, open free of charge to the public. We might even see extinct species. Dinosaurs roam in many zoos now (**Plate 15.1**), and appear to be as popular as the living collection. It is even possible that one day we might see sabre-toothed cats, mammoths, dodos, and thylacines (Nicholls 2009) (see also **Box 15.1**).

---

[3] **IMAX** is a registered name, and is an abbreviation for **IM**age **MAX**imum.
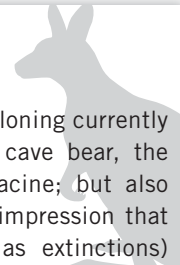
15.3 Sustainability

The United Nations has declared the decade 2005–2014 the Decade of Education for Sustainable Development (DESD). Increasingly, zoos see themselves as leading contributors to public education about sustainability. But is the zoo industry itself sustainable and, if not, what can it do to become so?

The concept of sustainability applies to zoos at a number of different levels. It can mean economic sustainability: will zoos still attract large numbers of paying visitors in fifty or a hundred years' time? But the word 'sustainability' nowadays is usually taken to mean environmental sustainability, and this can operate at an organizational level (which is about the sustainability of the practices that the organization undertakes) and, in the zoo context, it is also about the sustainability of the living collection itself (Dickie 2009), a topic which has already been introduced in **section 9.7**. We are now accustomed to issues about habitat loss, pollution, hunting, and so on as factors involved in biodiversity loss and habitat degradation, but now we also have climate change on the agenda. Can zoos, for example, meet the challenge of becoming 'carbon-neutral' organizations in the way that many big businesses[4] are now pledged to do? And what are the consequences of climate change for the living collections? Warnings that changes in temperature, indeed in climate generally, might provide the conditions for 'emergent infectious diseases' to become more prevalent (Barbosa 2009) tell us that the ramifications of environmental change in the future might be more extensive and insidious than many of us realize.

Zoos are certainly making strides in this direction. Chester Zoo in the North of England has as its mission and vision statement '*A diverse, thriving and sustainable natural world*', and Auckland Zoo in New Zealand offers 'sustainability tours' and advice to local businesses on how to reduce their carbon footprint.

15.3.1 Sustainability in sourcing animals

Good zoos are striving to achieve sustainability in their animal collections, with zoos becoming a growing source of animals *for* the wild, rather than *from* the wild. Accredited zoos have already made great strides in reducing the number of animals taken from the wild, and the goal of zoos within BIAZA, EAZA, AZA, and ZAA remains the management of self-sustaining populations in captivity (Conway 2007). We have already seen (see **sections 9.7** and **10.3.5**) that too many captive populations are actually not currently sustainable, and in some parts of the world, such as Australasia, this problem is exacerbated by import restrictions preventing the movement of animals between zoos in different countries (Lees and Wilcken 2009). Again, however, we should be wary of making generalizations. Legislation to prevent importing wild birds into the EU, for example, which was introduced to combat the threat of avian flu, has actually been beneficial as a driver of improved breeding practices (Walter *et al.* 2009). Similarly, the sustainability of the butterfly trade is generally good, and supplies animals for the many walk-through butterfly exhibits (Veltman 2009). Conversely, the sustainability of plant acquisition has not generally received as much attention as that of animals (Frediani 2009).

15.3.2 Sustainability in the day-to-day operation of the zoo

So what would a sustainable zoo look like? There have been many recent developments

---

[4] In the UK, the retailer Marks and Spencer announced in 2012 that it had achieved its goal of becoming a carbon-neutral organization; Google claims to have been carbon neutral since 2007.

Figure 15.6 This photograph shows the large and well-used Conservation Education Centre at Marwell Zoo (part of the Marwell Preservation Trust), in Hampshire, UK. The centre was built using environmentally friendly materials, such as wood from sustainable sources and low-emission paints, and makes good use of a variety of energy- and water-saving devices. (Photograph: Sheila Pankhurst)

in bringing about increased organizational sustainability in zoos, including the implementation of management systems, some of which, such as that set up at Paignton Zoo Environmental Park, UK, achieve the standard ISO14001 (Turner 2009). At the level of the individual zoo, we can imagine that the sustainable zoo will have some, if not all, of the following characteristics: a policy of not sourcing animals from the wild unless from sustainable sources; the sourcing of food locally (within 20, or at most 50, miles for both zoo visitors and zoo animals); energy sourced renewably and locally, and the installation of local energy generating schemes such as wind turbines and solar panels; buildings that are energy efficient, with high levels of insulation and ground storage heating or cooling systems; the use of rainwater and 'grey water' for toilets and irrigation, and other water-saving initiatives such as waterless urinals; green roofs; discounted parking charges for hybrid cars; campaigns for better public transport links and provision of bicycle stands; greater use of local materials, and wood from sustainable sources for buildings (**Fig. 15.6**); a zoo gift shop and restaurant that sell a high proportion of locally produced (and fair trade) goods (e.g. Koldewey *et al*. 2009; Sigsgaard 2009) (**Plate 15.2**); one or more recycling centres within the zoo (**Fig. 15.7**); and zoo signs that provide information not only about animals and their habitats, but also about sustainability.

In fact, these goals are already a reality in various zoos around the world (**Box 15.2**).

Figure 15.7 The next challenge towards which zoos are working is reducing their impact on the environment, which can be achieved by moving towards sustainable operating systems, including recycling. (Photograph: Paignton Zoo Environmental Park)

Box 15.2 SUSTAINABILITY IN ZOO PRACTICE

In **section 15.3.2** we mentioned some of the ways that sustainable practices are becoming more prominent in zoo operations. Here are some examples.

At Apenheul Primate Park in the Netherlands, for example, car parking is free of charge for hybrid cars. The Living Rainforest, UK, has its own biofuel boiler, which runs on locally produced (and carbon-neutral) wood chips. Artis Zoo in Amsterdam operates a sophisticated combined heat and power (CHP) system. At Edinburgh Zoo, a reed-bed system filters waste water.

Perth Zoo in Australia has a renewable energy display, which is part of a larger environmental programme with a grid-connected photovoltaic installation and a small demonstration wind turbine; Adelaide Zoo has a photovoltaic system on the roof of its panda exhibit, to provide a proportion of the energy needs of the building. The three zoos that make up Zoos Victoria in Australia (Melbourne Zoo, Werribee Open Range Zoo, and Healesville Sanctuary) achieved their goal of becoming carbon neutral in 2012. Over recent years, Wellington Zoo in New Zealand has reduced the waste sent to landfill from more than 90 per cent of its total waste to less than 20 per cent.

In North America, Cincinnati Zoo has waterless urinals, and has also installed a wind turbine which, in combination with solar panels, meets nearly a quarter of the energy demand for its ticket office and membership building (WAZA 2010). The Bronx Zoo in New York has an Eco-Restroom (toilet block) where all the grey water is reused for irrigation; the Zoo estimates that this saves a million gallons of water each year. At the North Carolina Zoo, biodiesel is produced using waste cooking oil from the zoo's restaurants.

In Canada, Toronto Zoo has developed what it calls Ice Bear storage technology. This is a power unit that uses energy at night, when demand on the grid is low, to freeze a giant block of ice. It then uses the ice during the day to cool the air for the building's air conditioning system. The Zoo also operates a geothermal unit, using heat stored in the ground, as an integral part of energy supply for the the lion-tailed macaques exhibit.

Zoo associations such as EAZA and BIAZA (see **Box 15.3** and **Fig. 15.8**) now make annual awards for sustainability initiatives. In North America, the AZA Green Award was established in 2011, and complements the AZA Zoo and Aquarium Green Award (AZA 2012).

Box 15.3 SUSTAINABLE AWARD-WINNING ZOO HORTICULTURE

Paignton Zoo Environmental Park in Devon has won a number of awards (from BIAZA in 2010, and the Norah Stucken Award from the Instititue of Horticulture in 2011) for its use of a vertical crop growing system to grow plants to feed the animals in the zoo.

As its name suggests, this is a space-efficient 'tower' system (**Fig. 15.8**), with a stack of trays in which crop plants such as lettuce are grown. Neither the use of vertical growing systems nor hydroponic culture is new, but the Zoo has chosen to put the three metre high system on show, rather than behind the scenes, to help educate visitors about alternative methods of food production, and ways of reducing food miles. One of the advantages of using this commercial growing system is that it requires only around 5 per cent of the normal water supply. It also uses less space than conventional growing systems. At Paignton the system grows 11,200 plants in a greenhouse of just 100m^2 (Bayley *et al*. 2010). As the Zoo says on its website, '*we can grow more plants in less room using less water and less energy*'.

Figure 15.8 The vertical growing system at Paignton Zoo Environmental Park, which grows crops on vertical racks using less space more efficiently. (Photograph: Geoff Hosey)

15.4 Careers in zoos

Jobs in zoos are more varied than many people first imagine. Of course, there are zookeepers and curators, but there are also zoo research officers, zoo education staff, zoo conservation officers, nutritionists, and a range of other staff.

The following is a brief overview of some of the main jobs in zoos that we have talked about in this book, with details of where you can find further information.

15.4.1 Zookeeper

Zookeepers nowadays are very likely to be graduates, or even postgraduates. If you want to become a zookeeper, you also need to demonstrate a real interest in—and, preferably, experience of—handling and caring for animals. This might include, for example, voluntary work at an animal shelter (**Fig. 15.9**).

The websites of keeper associations such as the Association of British Wild Animal Keepers (ABWAK), the Australasian Society of Zookeeping (ASZK), and the American Association of Zoo Keepers (AAZK) are a good place to start if you are interested in becoming a zookeeper. (The AAZK website has a useful page on zookeeping as a career at **http://www.aazk.org/zoo_career.php**.)

15.4.2 Zoo veterinarian

Becoming a zoo vet (**Fig. 15.10**) can take a long time. Typically, students enrolling on a veterinary medicine course in the UK will study full time for either five or six years, although some colleges now offer an accelerated veterinary medicine course (usually over four years) for students who
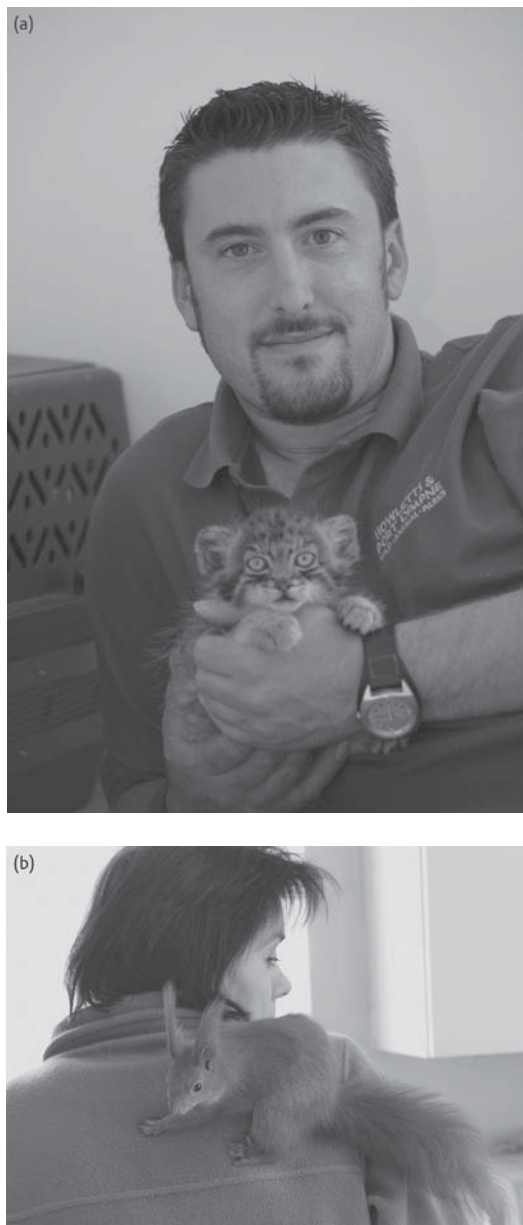
Figure 15.9 If you want to work with animals as a zookeeper, you will need to be able to demonstrate relevant experience, such as voluntary work at an animal shelter. These photographs show (a) keeper Ben Warren with a Pallas kitten *Otocolobus manul*, at Howletts Zoo, UK; and (b) a keeper at Warsaw Zoo with a hand-reared red squirrel *Sciurus vulgaris*. (Photographs: (a) Dave Rolfe, Howletts Zoo; (b) Barbara Zaleweska, Warsaw Zoo)

have already completed a BSc in the biological sciences.

An alternative degree is the BSc in Veterinary Surgery (BVS). Membership of the Royal College of Veterinary Surgeons (RCVS), which entitles the member to add the designation MRCVS after their name, is a legal requirement in the UK before a holder of a BvetMEd or VetMB degree can practise as a veterinarian (see **http://www.rcvs.org.uk** for further details).

In North America and Australia, training for a zoo vet is a similarly lengthy process. All veterinarians in the USA are required to complete a Doctor of Veterinary Medicine course (DVM or VMD) at a veterinary school which is accredited by the American Veterinary Medical Association (AVMA). This is typically a four year course, and usually follows on from an undergraduate training in a subject area such as zoology. Requirements for a BSc or other degree prior to entering the DVM programme vary from state to state, but in practice it is difficult to gain a place at veterinary school without a thorough undergraduate training in the life sciences. In Australia, you can only become a vet after studying at one of the seven universities currently offering a degree in veterinary medicine; this is usually six years of full time study.

Of course, qualifying as a vet is only the first step towards working with wild animals in a zoo. For qualified veterinarians in the UK, the RCVS offers both a postgraduate certificate and diploma courses in animal welfare science, **ethics**, and law.

15.4.3 Zoo veterinary nurse/assistant/technician

At the time of writing this book, there are no specific qualifications available in the UK for veterinary nurses working with wild animals in a zoo, although the Zoological Society of London (ZSL) sometimes offers summer work experience placements for veterinary nurses and trainee veterinary nurses. For further details, see **http://www.zsl.org**. In Australia, training for veterinary nurses is via the Veterinary Nursing Council of Australia; the
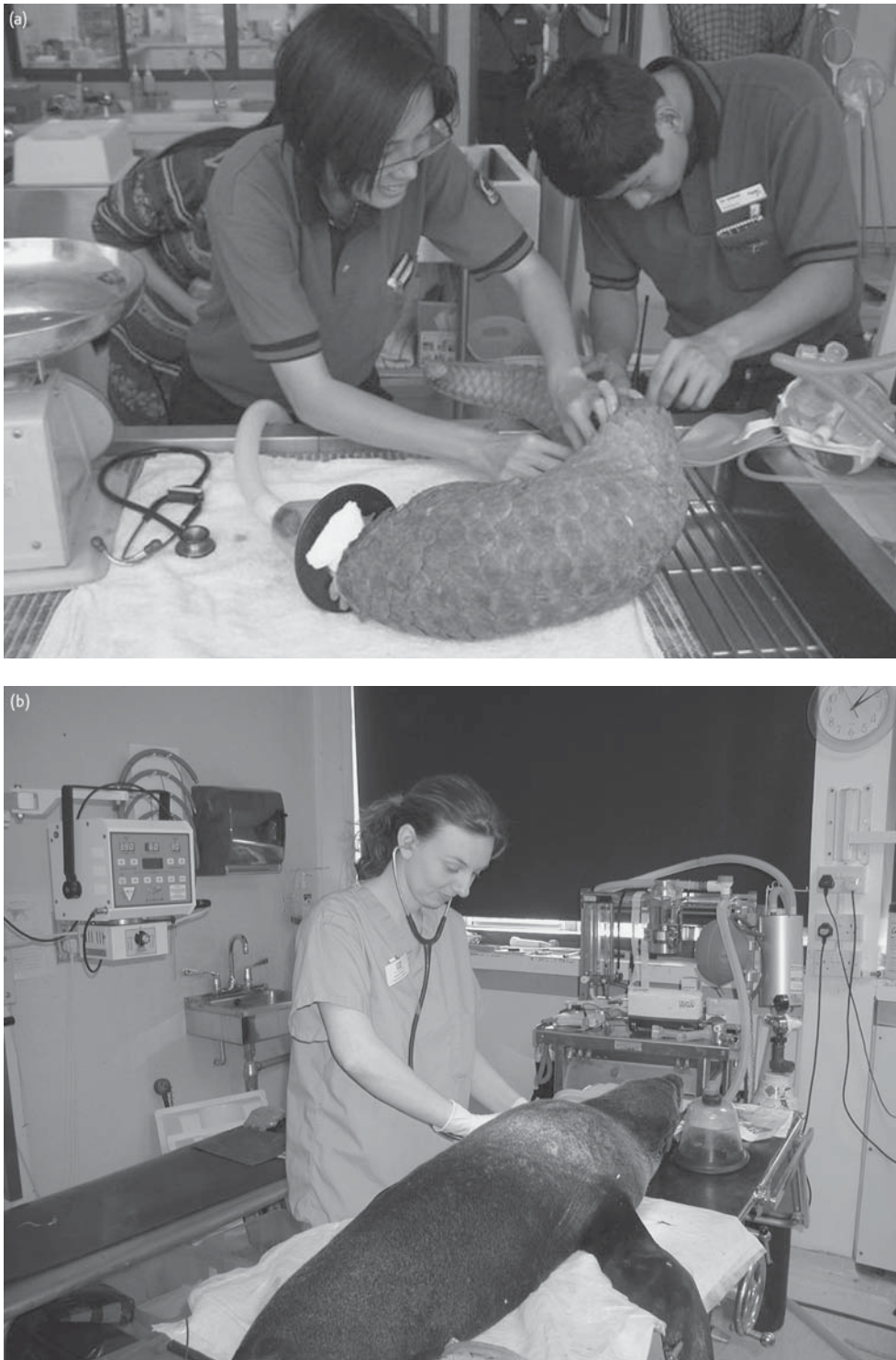
Figure 15.10 Working as a zoo vet is a challenging job: a typical medium-sized zoo may contain around a thousand animals from upwards of 300 species. Here, vets at Singapore Zoo and Bristol Zoo are examining (a) a pangolin *Manis* spp. and (b) a fur seal pup *Arctocephalus* spp., respectively. (Photographs: (a) Biswajit Guha, Singapore Zoo; (b) Mel Gage, Bristol Zoo)

website of the Council is at **http://www.vnca.asn. au/**. Again, there is no specialist training for work as a zoo veterinary nurse.

In America, you can train either as a veterinary assistant or as a more senior veterinary technician (a 'vet tech'); the latter requires either associate degree training, or enrolment on a veterinary technology bachelor's degree programme. The website of the National Association of Veterinary Technicians (NAVTA) provides useful information at **http://www.navta.net/**.

15.5 Challenges for the future

We hope that we have demonstrated in this book that the management of zoo animals, and indeed the whole operation of the modern zoo, is supported by an increasingly extensive body of empirical evidence, which informs best practice and evaluates the efficacy of procedures. Of course, new initiatives arise which still need this evaluation, and established procedures may need to be revisited in the light of new evidence. Here we look briefly at a few current issues which fall broadly within this category.

15.5.1 Breed and cull?

In recent years there has been much debate within the zoo community, and beyond, about the management of surplus or 'unwanted' animals, and particularly the adoption of a deliberate policy of 'breed and cull'. This is a management system which allows animals to breed, but culls the 'surplus' offspring, preferably at an age which would be significant in their life history in the wild, such as just after birth or at the time when they would disperse from their parents. Humane euthanasia is not a welfare issue, and this practice is already widely used in livestock farming (for example, male calves produced in order to prolong milk production in dairy cows are routinely culled), not to mention in the management of huge numbers of unwanted pets.

Adoption of this approach to management of animals in zoos allows the expression of their breeding and offspring rearing behaviour, but also resolves the problem of, for example, the need to house bachelor groups of animals such as gorillas or zebras, or of trying to find homes for the offspring of species such as lions and bears, which breed well in captivity but require a large amount of space and can live for a long time. Therefore it can also free up space for animals of greater conservation importance, and (although it sounds counter-intuitive) can lead to an enhanced quality of life for all of the animals, which as a consequence of the policy have enhanced ability to perform more of their natural behaviours (Jamieson and Portas, no date).

Although the culling of surplus livestock is widely accepted in farming, there has been a public outcry on a number of occasions when a similar practice has occurred or is proposed for zoo animals. Nevertheless, 'breed and cull' is already practised in a number of European zoos, and is supported by zoo organizations such as EAZA when animals cannot be adequately re-housed. Managed humane euthanasia should also be an option for geriatric animals, particularly if they have developed problems which potentially or actually affect their quality of life, and even of newborn animals who are not being cared for by their mother. Thus, managed humane euthanasia should be seen as part of an animal management strategy, and there is no reason why it could not be presented as such, and more positively, to the public. The case of Knut the polar bear *Ursus maritimus* (see **Box 15.4**) highlights this dilemma.

15.5.2 What are the welfare consequences of close encounters with animals?

We have already spent some time considering whether the presence of people in the zoo affects the animals in a significant way, and particularly if it has consequences, whether good or bad, for their welfare (see **section 13.3**). Many zoos now go beyond just keeper talks towards more interactive shows in which they may handle animals, and the animals may perform various activities (see

Box 15.4   WHAT SHOULD WE DO WITH AN UNWANTED BABY ANIMAL? THE CASE OF KNUT

When a zoo hits the newspaper or television headlines, this is usually in relation to public concerns about the welfare of the animals, although births in captivity of charismatic mammals such as elephants, tigers, or bears can also make the front pages. But some such births can also generate problems, as in the case of Knut (**Fig. 15.11**).

Born in 2006, Knut the polar bear cub was rejected by his mother. If a baby animal cannot be reared by its mother, what should the zoo do? One sensible option would be to euthanize the baby humanely, as its welfare could easily be compromised by the lack of a mother. In the case of Knut this suggestion was made. But there may be overwhelming public pressure for the animal to be kept alive and hand-reared, particularly if the young animal happens to be perceived as cute and appealing, and this is what happened in the case of Knut.

After German newspapers ran a story suggesting opposition (from an animal rights activist) to keeping the cub in captivity, and proposing euthanasia instead, there was a tremendous outpouring of public support for hand-rearing the cub. Visitor numbers, and income from the gate, rose sharply at Berlin Zoo, where the cub was housed, and Knut became something of a media sensation (dubbed 'Knutmania').

Knut died unexpectedly in 2010, at the age of four, after collapsing and drowning in the pool in his enclosure.

Figure 15.11 Knut the polar bear, who epitomizes the controversy over what to do with unwanted young animals (Photograph: Jean-Luc 2005/CC-BY-SA)

section **6.1.3** and **13.2.2**). Indeed, some of the more extreme versions of these interactive shows may require keepers to work in unprotected contact with potentially dangerous animals such as tigers. There is some evidence that keepers generally consider this to be unwise, at least in the case of the tigers (Szokalski *et al.* 2012b); this concern is certainly warranted, as between 1998 and 2001 seven people were killed and at least twenty-seven injured by captive tigers in the United States, although most of these were privately owned animals (Nyhus *et al.* 2003).

The other side of this particular coin is that we have very little idea of whether these shows affect the welfare of the animals. The only empirical data we have comes from dolphin shows (Miller *et al.* 2011b; 2013), and these suggest that the shows may well be enriching for the animals.

Interactive shows are very popular, and can generate a lot of funding for conservation and other activities, but clearly more studies are needed to assess their effects on the animals.

15.5.3 What can good zoos do about bad zoos?

Good zoos have no direct control over what goes on in poor zoos, unless the substandard zoo is one which wishes to engage with the accredited zoo community. However, good zoos can exert some influence on national governments, and bodies such as the EU and zoo associations such as EAZA have also been vocal in their calls for greater government intervention to deal with 'bad zoos'.

A recent change in zoo association policy, at least in the case of EAZA, has been to allow a new

category of membership for zoos which don't meet high standards of husbandry and welfare, but are committed to working towards achieving these. The EAZA Candidate for Membership category is aimed at substandard zoos (in Eastern Europe), and provides a framework through which they can be supported by the EAZA Technical Assistance Committee. Often, this is by providing training for zoo staff in other countries; a recent example of this is the training, by EAZA, of eighty zoo workers in Romania where, currently, there are no EAZA members.

Summary

- Zoos today understand that it is not enough to state a commitment to conservation and education; their achievements in these areas need to be evaluated against clear objectives.

- As well as striving to become effective centres for conservation, many good zoos are committed to sustainability and want to be seen as organizations that can take a lead in demonstrating sound environmental management.

- The shape of collections will continue to change, with a greater emphasis on the captive breeding of endangered species, and, in particular, species from non-mammalian and non-avian taxa.

- Zoos will increasingly have to justify, in the face of a sometimes hostile media and public, decisions to cull 'surplus' animals where adequate alternative housing cannot be found.

Questions and topics for discussion

1. What are the practical obstacles that may prevent a zoo from becoming a 'fully sustainable organization'?
2. Should zoos keep fewer mammals and more animals from other taxa? If so, why?
3. How can a zoo evaluate the effectiveness of its educational programmes?
4. To what extent should good zoos be responsible for solving the problem of bad zoos?
5. Discuss how zoos can become better at evaluating the impact of their conservation initiatives, rather than only measuring inputs.

6. Discuss the statement that '*humane euthanasia of surplus zoo animals is not a welfare issue*'. What are the main ethical considerations that need to be taken into account if zoos adopt a policy of '*breed and cull*'?

Further reading

In the previous fourteen chapters of this book, we have provided subject-specific suggestions for further reading, along with details of where to find further information on aspects of zoos ranging from legislation to enrichment. In this chapter, we want to do something rather different, and to recommend a few of the books and papers about zoos that have particularly interested, inspired, informed, and entertained us.

First and foremost, we strongly recommend Colin Tudge's thoughtful and well-written *Last Animals at the Zoo* (1992), which has the subtitle *How Mass Extinction Can Be Stopped*. Although published more than two decades ago, Tudge presents a well-argued and still relevant case for the conservation role of modern zoos.

The second book that we have enjoyed reading and would like to recommend is Gerald Durrell's *The Stationary Ark* (1976)—an account of the creation of Jersey Zoo. Re-reading this book recently (it was first published more than 30 years ago), we were struck by Durrell's foresight in some of his recommendations about how a modern zoo should operate. For example, in *The Stationary Ark*, Durrell said that zoo animals should be provided with '*an adequate diet, which is considered interesting by the animal*

and nutritional by you' and '*as much freedom from boredom as possible, i.e. plenty of "furniture" in the cages*'. All of this pre-dates the first version of the Secretary of State's Standards of Modern Zoo Practice (SSSMZP) by more than 25 years.

Douglas Adams and Mark Carwardine collaborated on the book *Last Chance to See* (1991), and a BBC radio series of the same name. *Last Chance to See* is an account of Adams' and Cawardine's attempts to see critically endangered species in the wild. Better known for books such as *The Hitchhiker's Guide to the Galaxy*, Adams (1952–2001) was a committed environmental activist. He and his co-author Mark Carwardine contributed a passage from their book *Last Chance to See* to another book, *The Great Ape Project*, written by Paola Cavalieri and the ethical philosopher Peter Singer (1994). The Great Ape Project became, in 1993, a wider campaign for equal moral rights for the great apes.

Susan McCarthy's *Becoming a Tiger: How Baby Animals Learn to Live in the Wild* (2005) is a very readable account of how animals learn, liberally sprinkled with anecdotes and examples. This is a book which you can dip into for information, amusement, and enjoyment.

Yann Martel's *Life of Pi* (2001) won the Mann Booker Prize in 2002. Pi, the hero of the book, is the son of a zookeeper in India. He later survives a shipwreck, only to spend 227 days at sea in the company of a Bengal tiger named Richard Parker. Unlikely, yes, but Pi's (Martel's) reflections on the animals in his father's zoo are well worth reading (many of the places described in this work of fiction are real, although there is no zoo in the Botanic Gardens at Pondicherry). The film of the book came out in 2012 to considerable critical acclaim. We would also like to point readers in the direction of a chapter entitled 'Conclusion: future of zoos' by Matthew Hatchwell and his colleagues in the book *Zoos in the 21st Century: Catalysts for Conservation?* (Hatchwell *et al.* 2007). Nicole Mazur concludes her book *After the Ark?* (2001) with a thoughtful chapter on 'Sailing into unknown waters'.

And last, but by no means least, we would like to end this book by singling out both a paper and a book chapter by Bill Conway (2003; 2007) for a cogent and clear-sighted view of the role of zoos in the twenty-first century.

For further self-assessment questions related to this chapter, please visit the book's Online Resource Centre.

http://www.oxfordtextbooks.co.uk/orc/hosey2e/

Glossary

A

abnormal behaviour   unusual or rare behaviour that may be pathological.

accredited zoo   a zoo that is licensed and a member of a national or regional zoo association (such as BIAZA, EAZA, AZA, ARAZPA, etc.).

activity budget   a quantitative representation of the proportion of its time that an animal spends in each of the behaviours or activities that it performs. This can be in the form of a table or a histogram (**Fig. 4.37**) (cf. **time budget**).

acute condition   a severe or aggressive illness that often develops quite rapidly (cf. **chronic condition**).

ad libitum (or ***ad lib.***)   free access; usually refers to food or water, indicating that the animal can choose to have as much as it wants.

adornment   object such as a tag, bead, ring, collar, or necklace, which is temporarily added to alter an animal's appearance so that it can be recognized.

agonistic behaviour   a behaviour that occurs in situations involving conflict or contests between animals. This includes both aggressive and submissive behaviours.

agronomy   the scientific study of crop production (including the study of soils).

allele   an alternative form of a gene. In individuals from sexually reproducing organisms, one allele, or copy, of each gene is inherited from the father and one from the mother. These alternative forms of a gene are responsible for determining traits (such as hair colour), and genes for some traits can come in many different forms or alleles. A stricter definition is 'an alternative form of a gene, found at a single locus (location) on a **chromosome**'.

altruistic behaviour   in the context of **ethology, altruistic behaviour** is costly for the individual animal or donor, but promotes the spread of the individual's genes by benefiting the recipient (i.e. increases the **direct fitness** of the recipient, but decreases the *direct fitness* of the donor).

analgesia   the relief of pain.

analgesic drug   a drug used to relieve pain.

Animal Health Veterinary Laboratories Agency (AHVLA)   an executive agency of Defra. The AHVLA was formed in 2011, following the merger of Animal Health and the Veterinary Laboratories Agency (VLA).

animal rights   animal rights campaigners generally hold that the rights of animals are equivalent to those of humans and that it is not acceptable to sacrifice the interests of one animal to benefit another (in other words, that humans should not be allowed to exploit non-human animals for their own purposes).

Annex A species   species listed in the first of four annexes to the EU Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) legislation. Annex A includes all CITES Appendix I species, as well as some Appendix II and III species for which the EU has adopted stricter measures than CITES.

anthelmintic (or **antihelmintic**) **drug**   a drug used to treat animals infected with parasitic gut worms, such as roundworms.

anthropoid ape   this term is rather out of date now (primate **taxonomy** has moved on). It refers to the 'man-like' apes—that is, the tailless primates, such as the chimpanzee, gibbon, gorilla, and orang-utan. Current taxonomy puts the chimpanzee, gorilla, and orang-utan, but not the gibbon, into the family Hominidae, along with humans.

anthropomorphism   the attribution of human qualities to animals (when there is no biologically valid evidence to do so).

anthropozoonotic disease   disease that can be transmitted from humans to non-human animals.

anti-pyretic   used to reduce fever (usually in the context of a drug)

anuran   member of the amphibian order Anura; frogs and toads.

Appendix I species   to a species listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). There are four appendices to CITES; Appendix I species are considered to be the most threatened.

appetitive behaviours   goal-seeking behaviours, whereas **consummatory behaviours** are goal-directed, or goal-oriented. Thus, searching for food is appetitive, whereas handling and eating food are consummatory.

approved vet   in the context of zoo licensing and legislation, an approved vet (AV) is a vet listed by the relevant local or national authority on a register of vets able to undertake zoo inspections etc.

aquaculture   the farming or cultivation of animals or plants that live in water (e.g. fish).

arboreal   refers to animals which spend most of their lives above ground, usually in trees.

Article 10 certificate   a permit needed by zoos within the EU to authorize the sale or movement of animals listed under Annex A of the EU legislation implementing the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

Article 60 certificate   a permit (formerly called an 'Article 30 certificate') that allows zoos to display their Annex A species and also to move them to other zoos within the EU, provided that the other zoos also have an Article 60 certificate.

artificial insemination (AI)   a reproductive technology in which semen is collected from one or more male animals prior to being inserted via a catheter into the vagina or another part of the reproductive tract of the female.

aversion test   test that studies if an animal is willing to choose to undergo something unfavourable, such as an electric shock, in order to gain access to a resource.

B

Balai Directive   a European Council Directive (92/65/EEC) governing the transport of non-domestic animals by EU member States (*balai* is the French word for broom—this Directive 'sweeps up' animals not covered by other EU legislation).

barren enclosure   enclosure with few, if any, objects or furnishings.

basal metabolic rate   the minimum amount of energy usage required to support life processes (cf. **metabolic rate**).

behavioural competence   the ability of an animal to express appropriate behaviour in a given situation.

behavioural diversity   a measure of the number and variety of behaviours that a particular individual shows.

behavioural ecology   an approach to studying animal behaviour that concentrates on how and why particular behaviours have evolved, and how they influence the individual's **fitness**.

behavioural economic theory   in the context of this book, this is where principles of economic theory, such as elasticity of demand, are applied to animal behaviour.

behavioural engineering (or **behavioural enrichment**)   a method of increasing animal activity by requiring them to perform a task for a reward.

behavioural husbandry   changes in the captive animal's environment that will impact on its behaviour, e.g. **enrichment** and training.

behavioural restriction   the inability of animals to express their full repertoire of behaviours.

Behaviourism   a scientific discipline that viewed mental events as unknowable and, in its most extreme form, even denied that they existed. This led behaviourists to study only observable behaviour, so that their view of animals was effectively of automata whose behaviour was shaped by **stimuli** through a process of operant conditioning.

binomial name (or **binomial nomenclature**)   the two-part scientific name for a species, comprising the names of the genus and the species. The genus name always starts with a capital letter, and the species name always starts with a lower-case letter. Both parts of the name are italicized (or underlined if handwritten)—e.g. the binomial name of a lion is *Panthera leo.* The binomial system of naming organisms was developed in the eighteenth century by the Swedish scientis Carl Linnaeus (the Latinized version of his name is Carolus Linnaeus).

bioavailability   the proportion of a nutrient that is available for physiological functions within the body. The bioavailability of some minerals can be reduced by antagonistic effects with other minerals, where the presence of one blocks the uptake or utilization of another.

biological control   the use of natural predators, parasites, or pathogens to control pest species.

biopark (or **BioPark**)   a zoo exhibit in which the animal is shown within a portrayal of its ecosystem (e.g. in a rainforest setting, or a desert setting).

biosecurity   steps to reduce the incidence and spread of disease.

birth rate   *See* **fertility**

body condition scoring   a subjective method of measuring or scoring the general body condition of an animal as an indication of its nutritional status and energetic state. This can be done visually or by handling the animal (e.g. by feeling the amount of fat over the vertebral processes of the spine).

bovid   a member of the family Bovidae (cattle, sheep, goats, antelopes, etc.).

bovine spongiform encephalopathy (BSE)   a form of **transmissible spongiform encephalopathy (TSE)** that causes degeneration in the brain and spinal cord of cattle.

branding   marking an animal's skin through the application of extreme heat or cold.

breed and cull   a management strategy in which animals are allowed to breed, but the group size is kept constant by selective culling of individuals within the group.

buccotomy   surgery, such as dental surgery, within the mouth cavity, where an incision is made in the cheek to gain access to the inside of the mouth

C

caecum   the large diverticulum (a sac with just one opening) in the gastrointestinal tract, at the point where the small intestine becomes the large intestine. All that is left of it in humans is the sometimes troublesome appendix.

cafeteria-style feeding (CSF)   a variety of foodstuffs are offered (e.g. a mixture of fresh fruits and vegetables) and animals are allowed to choose what they consume (cf. **complete feed-style feeding**).

callitrichid   a species of small New World monkey of the family Callitrichidae, or more correctly now the sub-family Callitrichinae, which includes the marmosets and tamarins.

captive assurance programme   *See* **captive management programme**

captive breeding programme   *See* **captive management programme**

captive management programme   the planned and managed breeding in captivity of a threatened species, involving cooperation between zoos within a country or region. Examples of captive breeding programmes include **European Endangered species Programmes (EEPs)** in Europe and **Species Survival Plans (SSPs)** in North America.

capture myopathy   the build-up of lactic acid in muscles during and after capture, which can cause stiffness, paralysis, and even death. Capture myopathy has been reported in a wide range of **taxa** and, in some cases, can cause death almost immediately, or up to a few weeks later.

carnivore   an animal that eats other animals (e.g. the tiger, the shark, the eagle) (cf. **herbivore**; **omnivore**)

Carnivore   a member of an order of mammals, the order Carnivora. This includes meat-eating animals such as lions and tigers, but also plant-eating giant pandas and omnivorous badgers. (Note the capitalization.)

cartilaginous fish   a fish with a skeleton made of cartilage rather than bone, of which the **elasmobranchii** is a sub-class including skates, rays, and sharks (cf. **teleost**)

causal (or **proximate**)   explanations of behaviour that attempt to identify its immediate causes, e.g. **stimuli**, motivational changes, hormone levels (cf. **functional**).

cellulose   a carbohydrate macromolecule used extensively by plants in their structure (e.g. as cell walls).

chaining (or **picketing**)   a method of restraining elephants, where one front and the diagonal back leg are chained, so that the elephant is able to move approximately one step forward and back.

charismatic megafauna   the animals—nearly always mammals—that have strong popular appeal, such as tigers, pandas, wolves, and elephants. These animals are often (but not always correctly) assumed to be the species that zoo visitors most want to see.

chelonian   a member of the reptilian order Chelonia, the tortoises and turtles.

chromosome   a length of DNA that contains genes and other elements. In animals that have cells with nuclei, the chromosomes are paired structures located in the cell nucleus (in humans, for example, there are normally forty-six chromosomes in each body cell, arranged as twenty-three pairs).

chronic condition   a condition that persists over a long period of time and which may require long-term management (e.g. diabetes) (cf. **acute condition**).

chronic wasting disease (CWD)   a form of **transmissible spongiform encephalopathy (TSE)** that causes small lesions in the brains of infected deer species, such as moose and elk.

classical conditioning (or **Pavlovian conditioning**) a form of **learning** in which the animal learns to associate an existing **response** with a new **stimulus** (e.g. showing food-related behaviours not to food itself, but to the sound of it being prepared) (cf. **instrumental conditioning**).

clinical   in the context of this book, relating to the observation, examination, and treatment of sick animals.

clinical sign   the visible sign of a possible disease or injury, such as a rash or a swelling.

coccidian parasite   a type of **protozoan** parasite (a small unicellular animal)

cognition   refers to the processes by which animals perceive, process, and store information. Cognition, broadly speaking, includes all of the ways in which animals take in information through the senses, process and retain this information, and act on it.

communicable disease   a disease that can usually (but not always) be passed on, or 'communicated', between animals or humans.

complete feed-style feeding   the provision of a processed diet that meets the nutrient requirements of the animal (but does not offer any choice) (cf. **cafeteria-style feeding**).

confounding variable   in studies of animal behaviour, a variable or factor that affects the results of a study, but which cannot be controlled (e.g. the weather, or an unexpected outbreak of disease).

consciousness   the awareness of one's own mental and/or physical actions. Dawkins (2006) offers the definition that '*consciousness refers to a wide range of states in which there is an immediate awareness of thought, memory or sensation*'.

conspecific   another animal of the same species.

consummatory behaviours   *See* **appetitive behaviours**

contrafreeloading   animals actively working for a resource in their enclosure, even when it is freely available.

coprophagy   the eating of faeces.

corticosteroids   a group of steroid hormones produced by the adrenal cortex (e.g. cortisol).

cortisol   a **corticosteroid** hormone produced by the adrenal cortex and involved in the body's **response** to stress (measurements of circulating cortisol levels are sometimes used as a measure of stress).

curative medicine   treatment of disease or injury (as opposed to **preventive medicine**, which seeks to prevent disease or injury).

D

demographics   the characteristics of a population, such as its age or sex structure, birth and death rates, and so on.

dendrobatid frogs   members of the family Dendrobatidae, also known as 'poison dart frogs'.

dietary drift   where diets are changed incrementally over time by keepers (not always for the better).

digestion   a process within which macromolecules that animals ingest as food are broken down into smaller molecules inside the gastrointestinal (GI) tract

direct fitness   a measure of the number of genes passed on to the next generation via an individual's offspring (cf. **indirect fitness** and **inclusive fitness**).

disease   a disorder or pathological condition of a body part or the whole organism, produced by an infection or genetic defect or other cause.

Disinfectant Era   the period from the 1920s onwards when zoo enclosures were designed primarily for ease of cleaning, rather than with regard to the needs of the animals housed within them. This trend for sterile, often minimalist, cages with concrete floors and tiled walls persisted well into the 1960s and 1970s.

displacement behaviour   behaviour that seems to be irrelevant to the **stimulus** situation in which it is performed.

dolphinarium   a facility that, strictly speaking, houses only dolphin species, which include the orca, or killer whale, *Orcinus orca* (cf. **oceanarium**).

double-clutching   a process whereby some, or all, of the eggs laid in one clutch are removed and incubated artificially, in the hope that the animal will lay another clutch and thus double its reproductive output.

dry matter   the weight of a quantity of a foodstuff without the water content.

E

ecosystem exhibit (or **ecosystem zoo**)   an exhibit or zoo that is designed to represent an entire ecosystem or ecosystems, rather than a single species or a group of animals displayed on **taxonomic** or regional lines (used interchangeably with the term **biopark** by some authors).

ectoparasite (or **exoparasite**)   a parasite that lives on the body of its host (e.g. a flea or a mite) (cf. **endoparasite**).

ectothermic   animals, sometimes referred to as 'cold-blooded', which regulate their body temperature by acquiring heat from external sources (cf. **endothermic**).

effective population   the number of animals that actually breed and contribute offspring to the population.

elasmobranch   *See* **cartilaginous fish**

electivity index   an index of the amount of usage by an animal of particular items or structures within its enclosure.

embryo transfer   technique in which embryos from wild mammals are transferred into a different species for gestation.

empirical study   a study based on observation rather than on what has been reported in the literature (data may be obtained from observing animal behaviour, for example, or from observing the results of an experiment).

endogenous stimuli   those **stimuli** that arise from within the animal (cf. **exogenous stimuli**).

endoparasite   a parasite that lives within the body of its host (e.g. a tapeworm) (cf. **exoparasite**)

endoscopy   diagnostic test using a small camera mounted on a flexible tube (endoscope) to look inside an animal's body, via the mouth.

endothermic   animals, sometimes referred to as 'warm-blooded', which regulate their body temperature through controlling internal metabolic processes (cf. **exothermic**).

enrichment   any change to an animal's environment that is implemented to improve the animal's physical fitness and mental well-being (cf. **environmental enrichment**).

environmental challenge   the presence or absence of properties within the environment that may act to overstimulate or understimulate the animal.

environmental enrichment   the provision of species-specific opportunities within an animal's environment to enable it to express a diversity of desirable behaviours.

epidemiology   the study of the incidence, prevalence, and treatment of disease in the population.

ethics   a narrower concept than morality, although the words are often used interchangeably. Ethics, strictly speaking, refers to a branch of philosophy that tries to clarify and analyse the arguments that people use when discussing moral questions.

ethogram   a list, with descriptions, of the behaviours observed in a particular species or group of animals.

euphagia   *See* **nutritional wisdom**

European Endangered species Programme (EEP) a planned and managed programme for breeding threatened species in settings such as zoos. In Europe, this is achieved via European Endangered Species Programmes (EEPs); in North America, it is achieved via Species Survival Plans (SSPs).

euthanasia   the humane killing of an animal if, for example, it is sick or badly injured.

evolutionarily significant unit (ESU)   a population that, for conservation purposes, is considered to be distinct—that is, the minimum unit for conservation management. The usefulness of the ESU concept is that it bypasses difficulties in defining species.

exogenous stimuli   those **stimuli** that arise in the environment outside the animal (cf. **endogenous stimuli**).

exoparasite   *See* **ectoparasite**

exotic animal   a very variable term, but generally used to mean a wild, rather than a domesticated, animal (so cats, dogs, and dairy cattle are not exotics). Whether an animal is exotic or not depends on your viewpoint and where you are in the world: camels may be regarded as exotics in the UK, but not in Egypt

***ex situ* conservation**   the conservation of animals outside their natural habitat, e.g. in zoos (cf. ***in situ* conservation**)

F

F2   a second-generation zoo animal—that is, a zoo animal that was born in captivity.

fecundity   a measure of reproductive potential (often measured as the number of gametes produced)

fertility   the actual reproductive performance of an organism, usually measured as the number of viable offspring (the term **birth rate** means much the same thing as fertility and the two terms are sometimes used interchangeably).

fitness   an indication of how well an animal is adapted to its environment. Fitness is usually measured in terms of the number of offspring of an individual animal that survive to reproductive age.

five freedoms   the standards of animal welfare developed by the UK's Farm Animal Welfare Council (1992). Freedom 1, for example, is freedom from hunger and thirst. Freedom 3 is freedom from pain, injury, or disease.

five principles   five basic principles of animal care and management, which form the basis of the standards set out in the UK Secretary of State's Standards of Modern Zoo Practice (SSSMZP). The 'five principles' are derived from the **five freedoms** of animal welfare.

flagship species   a species that can excite public attention, and can therefore also raise public support and perhaps generate funds.

flehmen   a behaviour shown by some mammals in which olfactory **stimuli** are detected by taking air into the mouth and, from there, into a specialized receptor—the vomeronasal organ—in the roof of the mouth. The behaviour is usually accompanied by the characteristic facial expression of mouth slightly open and upper lip retracted.

flight distance   the distance at which an animal will not allow an aversive **stimulus** (e.g. a person) to come any closer, usually the point at which the animal will flee.

flight restraint (or **wing management**)   physical modifications to a bird's wing that prevent it from flying.

fomite   an inanimate object that can spread disease from one individual to another. In zoos, a fomite might be a contaminated bucket or food bowl, or a keeper's boots.

forage   a general term for any kind of fodder made out of herbaceous plants, such as hay, straw, silage, etc.

formal learning   **learning** from structured experiences, such as keeper talks, demonstrations, or short courses (cf. **informal learning**).

founders   individuals from which populations derive.

free-ranging   a term used in a variety of ways, but usually to imply that the animals are not restricted in where they go, although, in reality, there will be restrictions at some point.

functional (or **ultimate**)   explanations of behaviour that attempt to identify why and how the behaviour has evolved (cf. **causal**).

G

gait scoring   the subjective scoring of measures such as the rate, direction, and range of movement of an animal, as well as the strength or force of its gait.

gallinaceous   (meaning 'chicken-like') birds such as pheasants, partridges, grouse, quails, etc. from the order Galliformes. They are usually ground-feeding birds and many species are hunted as game birds.

gene pool   all the genes in a given population of a species.

genetic diversity   broadly, the number of different genetic characteristics in a population. These genetic characteristics can be the genes, or the chromosomes, or the entire genome (or even the nucleotides that make up genes).

genotype   the genetic constitution of an individual (cf. **phenotype**).

giraffid   a member of the family Giraffidae, the extant members of which comprise the giraffes and the okapi.

gut microflora   a general name for the micro-organisms that inhabit the digestive tract.

H

habituation   a form of **learning** in which the animal reduces its **response** to a constant or repetitive **stimulus**.

ha-ha   a ditch separating two areas, such as an animal enclosure from a visitor area.

haemochromatosis   iron-storage disease.

haemosiderosis   increased iron storage in the body tissues (benign, rather than disease-causing).

helminth   a species belonging to a range of genera of multicellular parasitic worms that inhabit the gastrointestinal (GI) tract and sometimes other parts of the body. Helminths include trematodes (or flukes), cestodes (or tapeworms), and nematodes (or roundworms).

herbivore   an animal that eats plants (cf. **carnivore**; **omnivore**).

herpetology   the study of reptiles and amphibians (known generally as **herps**).

herps   a general term used to describe reptiles and amphibians.

heterozygous   having two different **alleles** of a gene (cf. **homozygous**).

hispid   covered with stiff bristly hairs.

homeostasis   the processes that maintain the animal's body in a stable state (or state of balance) so that it can carry out necessary survival functions.

homeothermic   maintaining a relatively constant body temperature, independent of the environmental temperature (mammals and birds are homeothermic, whereas fish,

amphibians, and reptiles are **poikilothermic** and their body temperature varies with that of their surroundings).

homozygous   having two identical copies or alleles of a gene (cf. **heterozygous**).

hormone assay   a method of determining the presence and/or amount of a hormone in a given sample.

husbandry guidelines (or **husbandry manuals**) guidance on the day-to-day care of an animal or species covering, for example, diet, space requirements, etc.

Hygiene Era   *See* **Disinfectant Era**

hypothalamo-pituitary-adrenal/gonadal (HPA/HPG) axis   the hormonal regulatory system that is common to the reproductive physiology of all vertebrates.

I

immersion exhibit (or **landscape immersion**) an exhibit within which landscaping includes the visitor area, so visitors get the sensation that they are in the animals' habitat (e.g. 'walking through a rainforest').

imprinting   a form of **learning** in which young animals learn about their species identity, sex identity, or relatedness to other individuals.

inbreeding   referring to when closely related animals breed with each other.

inbreeding depression   a situation in which **inbreeding** results in offspring with reduced genetic diversity, because both parents have provided similar genetic material.

induced ovulator   an animal in which the release of an egg or ovum by the female is stimulated by the act of copulation with a male.

informal learning   the acquisition of knowledge without formal instruction, e.g. by reading zoo signs (cf. **formal learning**).

***in situ* conservation**   the conservation of animals within their natural habitat—that is, 'in the wild' (cf. ***ex situ* conservation**)

instrumental conditioning (or **operant conditioning**) a form of **learning** in which the animal acquires a new **response** to an existing **stimulus** (e.g. pressing a lever in order to get food) (cf. **classical conditioning**).

integrated conservation the bringing together of different activities and different agencies in order to achieve conservation priorities.

integrated pest management a broad approach to pest control, which includes the use of biological controls, changes in husbandry to prevent access by pests, etc., to reduce the need for the use of more radical interventions such as pesticides.

inter-birth interval calculated as the time between births, which is recorded from the birth of the first offspring until the birth of the second offspring.

inter-observer reliability a statistical test to measure the strength of agreement between two or more observers measuring the same parameter.

invasive procedure a veterinary (medical) procedure that 'invades' the body, such as blood sampling.

in vitro* fertilization (IVF)** the production of an embryo in culture in the laboratory or clinic (cf. ***in vivo fertilization).

in vivo* fertilization** the production of an embryo inside the mother's body (in the case of mammals and birds) (cf. ***in vitro fertilization).

isozoonosis a disease that shows very similar pathology in both humans and animals.

L

lamellibranch a bivalve mollusc belonging to the class Lamellibranchia (e.g. scallops and clams).

landscape immersion *See* **immersion exhibits**

latency the time gap between a **stimulus** or event and a **response** occurring—e.g. if a novel object is placed in an animal's cage and the animal first approaches the object after three minutes, the latency to 'approach novel object' is three minutes.

learning the process that takes place when an experience of some sort brings about a relatively permanent change in the way in which an animal responds to a situation.

life history traits the characteristics of a species, such as age at weaning or fledging, age at first reproduction, number and size of offspring, reproductive lifespan, adult survival, and ageing. In a bird species, for example, clutch size and re-nesting rate after clutch failure would both be examples of life history traits.

longevity a measurement of the length of time that an animal lives (also a useful indicator of how well an animal has been able to survive and thus succeed).

M

macropod animal belonging to the marsupial family Macropodidae (such as kangaroos, wallabies, and tree kangaroos).

maintenance rations referring to when the amount of energy entering the animal is equal to the amount leaving the animal.

malnutrition not necessarily a shortage of food *per se*, but a deficiency or deficiencies in **nutrients** in the diet.

mean kinship a value that describes an animal's genetic representation in the population. Animals with a low mean kinship (close to 0) are related to fewer animals than those with a high mean kinship. Thus, an animal with a mean kinship of 0 is not related to any other animals in the population.

menagerie this comes from the French word *ménage*, meaning a household or unit of people living together. The word *ménagerie* was used from the sixteenth century onwards in France to refer to the management of a farm or collection of livestock and gradually came into use to refer to a collection of exotic animals.

metabolic rate the amount of **metabolizable energy** expended by an animal over a given period of time—i.e. energy metabolism per unit time.

metabolizable energy (ME) the energy content of the food taken in by an animal; a measure of the energy available to satisfy the animal's metabolic requirements.

metapopulation a collection or network of sub-populations that are connected in some way. The links between the sub-populations are usually immigration and emigration from one sub-population to another. Thus, the groups of animals housed in different zoos can be regarded as sub-populations of a larger metapopulation, which also includes the wild population, if there is transfer of animals between sub-populations.

mixed-species exhibit an exhibit housing more than one species.

modality the way or mode in which something is done. *See also* **sensory modality**

monkey chow   food concentrate designed to provide a complete and balanced diet for monkeys

monogamy   a pairing between one male and one female, particularly in those species among which male desertion is not profitable because females are unable to raise the young alone (e.g. many birds). A distinction needs to be made between social monogamy and genetic monogamy (the male in a social pair may not always be the father of some, or all, of the female's offspring) (cf. **polygamy**, **promiscuity**)

monogastric   a non-**ruminant** animal with a single-chambered stomach (e.g. bear, human).

morbidity   the incidence of disease, or the number of animals that will become sick.

mortality   the death rate from a disease.

N

natural selection   the process, observed in wild animal populations, whereby the alleles of some 'fitter' animals are transferred into the next generation, whereas the alleles of 'less fit' animals are not.

naturalistic enclosure   an enclosure that attempts to replicate the animals' natural habitat through the appropriate use of land formations and plant life.

necropsy   a **post-mortem** examination to try to determine the cause of death.

negative reinforcer   a **reinforcer** that involves removal of a **stimulus**, such as turning off an electric shock (cf. **positive reinforcer**).

neophilia   the attraction to novel objects or new situations (cf. **neophobia**).

neophobia   the avoidance of novel objects or situations (cf. **neophilia**).

notching   making carefully placed holes or marks in the animal's horn, shell, scales, or ears to act as an identifier.

notifiable disease   a disease that must be reported to the relevant authorities. In the UK, a notifiable disease must be reported to the police; in practice, Defra should also be notified. Examples in the UK include rabies, anthrax, and foot-and-mouth disease (FMD).

nutrient   a substance needed for the survival and growth of an organism.

nutrition   a process that occurs within organisms of taking in and absorbing **nutrients**, to provide energy and to meet other metabolic needs

nutritional requirements   the particular elements or compounds that an animal must have in its diet in order to satisfy all of its requirements for growth, and for building and maintaining its metabolic machinery.

nutritional wisdom (or **euphagia**)   the idea that animals can select a balanced diet by detecting the nutritional quality of the different foods that they encounter.

O

obstruction test   a test in which an obstruction, such as a door or steep ramp, is placed between the animal and a resource in order to determine how hard the animal is willing to work to get around the obstacle to gain the resource.

oceanarium   a marine animal park housing species such as seals, sea lions, dolphins, etc., and sometimes also fish, corals, and other marine life (cf. **dolphinarium**).

omnivore   an animal that eats plants and animals (cf. **carnivore**; **herbivore**)

operant conditioning   *See* **instrumental conditioning**

organic   refers to carbon-based compounds, which usually also contain oxygen and hydrogen. These compounds are not necessarily the result of living processes. (The term can also refer to an agricultural system.)

oviparous   meaning egg-laying (cf. **viviparous**)

P

pachyderm   a non-**ruminant** hoofed animal with a very thick skin, such as a rhinoceros, hippopotamus, or elephant. The word is no longer used as a **taxonomic** term.

passive integrated transponder (PIT)   a microchip containing a unique magnetic code, which is usually injected just beneath an animal's skin and is used to code its identity.

parthenogenesis   reproduction where an unfertilized egg or ovum develops into a new individual.

Parthenogenesis is relatively common among invertebrates but rare in vertebrates.

pathogen   disease-causing agents (from *patho* meaning disease), such as bacteria, viruses, fungi, or other organisms such as protozoan parasites. The **prions** that cause **bovine spongiform encephalopathy (BSE)** and other **transmissible spongiform encephalopathies** are pathogenic proteins.

pathology   the study of disease (hence **pathological**; a **pathologist** is someone who studies disease).

Pavlovian conditioning   *See* **classical conditioning**

Perissodactyla   commonly referred to as 'odd-toed ungulates', of which there are two sub-orders: Hippomorpha and Ceratomorpha. Equidae are the only family of Hippomorpha, and Tapiridae and Rhinocerotidae represent the two extant families of Ceratomorpha.

perseveration   an animal's carrying on of an activity in the absence of the appropriate **stimulus**.

pest   a species (plant or animal) that occurs where it is unwanted.

petting zoo   an area that usually contains domesticated or habituated animals, with which visitors are allowed to come into close contact.

phenotype   the product of interaction between an individual's **genotype** and the environment in which it develops. This effectively refers to what the individual looks like and how it behaves.

phylogeny   describes the evolutionary relationships between a set of species or other taxonomic grouping.

pica   in humans, often used to refer to the consumption of non-food items—from coal to soap—but can also mean cravings for particular food constituents.

picketing   *See* **chaining**

pinioning   a form of **flight restraint** involving the amputation of a digit at the wing tip.

plane of nutrition   level of nutrition. An animal with a high plane of nutrition has ready access to a high-quality diet, in which food is not in short supply. In the zoo situation, this can sometimes lead to problems such as obesity.

plant secondary metabolite (PSM)   a substance that acts to make a plant distasteful or even toxic, or which may make it difficult for the animal to extract the important **nutrients**. PSMs are so-called because they are synthesized from the products of ordinary or primary metabolism.

poikilothermic   an animal whose body temperature varies with that of the environment (cf. **homeothermic**).

polyandry   a mating system, unusual in mammals, in which a female has several male mates or partners in a breeding season. Examples of species among which polyandry is found include the jacanas (a group of wading birds) and several frog species (cf. **polygyny**).

polygamy   a general term for mating systems in which one individual of one sex mates with several individuals of the other sex. Thus it includes both **polygyny** and **polyandry** (cf. **monogamy**, **promiscuity**).

polygyny   the mating of one male with many females. It occurs particularly in species among which females are able to raise young with little male input (e.g. many mammals, in which gestation and lactation facilitate male desertion).

population genetics   the study of the change in frequency of **alleles** in a population over time, as a result of processes such as natural selection, genetic drift, mutation, and gene flow.

positive reinforcement training (PRT)   the use of operant conditioning techniques in which animals are rewarded for exhibiting the behaviours that the trainer wants them to exhibit.

positive reinforcer   a reward that follows a required **response** (e.g. the provision of food) (cf. **negative reinforcer**).

post-mortem   the examination of a dead animal, or tissues from a dead animal (literally meaning 'after death'). Often used informally to mean **necropsy**.

post-occupancy evaluation (POE)   a technique used to assess how animals use their environment (e.g. their enclosure space).

preference test   a test that attempts to measure an animal's preferences (e.g. for different foodstuffs) objectively.

preventive (or **preventative**) **medicine**   a branch of veterinary (or human) medicine that tries to prevent disease from occurring. In zoos, preventive medicine includes measures such as regular health checks, quarantine procedures, good enclosure hygiene, etc.

prion   a disease-causing agent or **pathogen** that is not a micro-organism, but a protein. Prions do not contain any genetic material.

promiscuity   a mating system in which both males and females have multiple sexual partners (cf. **monogamy**, **polygamy**).

protozoan   unicellular organism, which includes free-living, as well as parasitic, forms.

proximate   *See* **causal**

pseudoreplication   the term usually used to describe data among which the sample points are not independent.

psittacine   refers to members of the avian order Psittaciformes, such as parrots, macaws, and lories.

punishment   in the context of animal training involving **operant conditioning**, **punishment** decreases the likelihood of a behavioural response occurring in the future.

Q

quarantine   a period of isolation for an infected animal, or to check for the possible development of an infectious disease (the word comes from the Latin for 40 days).

R

randomization test   also called a permutation test, this calculates a test statistic and compares it with the results from repeated randomization of the same data across all groups

regional collection plan (RCP)   a plan drawn up by a regional zoo association, such as EAZA or the AZA, to inform member institutions on which species they should be keeping and how they should manage them. The RCP may also identify species that should (preferably) not be kept.

regurgitation/reingestion   behaviour shown in some captive gorillas where food is voluntarily brought back up from the stomach to the mouth, or on to a substrate, and is then reswallowed.

reinforcer   any event that increases the probability of a particular **response** (*see* **positive reinforcer**)

reintroduction   the intentional movement of an organism into a part of its native range from which it disappeared or became extirpated in historic times as a result of human activity or natural catastrophe.

response   the behaviour that an animal shows when stimulated by an event (**stimulus**) in its environment.

reversed lighting schedule   a schedule that maintains illuminated conditions during natural darkness and darkness during natural daytime, used to exhibit nocturnal species (those that are active during darkness).

reverse-reward contingency tasks   animals are given an option of a small and a large reward; they have previously been trained that if they choose the small reward, they will in fact receive the large reward. In essence, animals which have 'control' are able to choose the small reward.

rumen   the first (and usually largest) of the stomach chambers of **ruminant** animals and a primary site for the microbial fermentation of ingested foodstuffs.

ruminant   a hoofed animal that 'chews the cud'—that is, regurgitates partially digested food. The stomach of ruminants is chambered.

S

scatter feed   feeding technique in which the animals' daily food ration, or part of it, is spread out around the enclosure.

scientific name   *See* **binomial name**

scoliosis   a side-to-side curvature of the spine.

self-awareness   the knowledge of oneself as an individual, distinct from other individuals. (Along with **theory of mind**, self-awareness is regarded as a higher-order cognitive ability and the extent to which animals possess these abilities is controversial.)

self-directed behaviour   behaviour that the animal directs towards its own body, such as scratching and body-shaking.

self-injurious behaviour (SIB) behaviour that damages one's own body (e.g. biting oneself); some authors include excessive hair- or feather-plucking within this term.

self-medication in the context of wild animals, whether in the zoo or in their natural habitat, the deliberate ingestion of plants or other material (e.g. soil or minerals) apparently to alleviate the symptoms of disease.

sensory modality (or **stimulus modality**) a type of information or physical phenomenon, and how this is presented to the senses. Examples are visual, auditory, olfactory, and tactile modalities.

sentience the ability to perceive and respond to the external environment; an alert cognitive state (sentience is often used to imply **consciousness**, but the ability to detect and respond to **stimuli** does not necessarily require consciousness). One of the best and simplest definitions of sentience is having '*feelings that matter*' (Webster 2006) and the word is often used in connection with animals' ability to perceive pain and to suffer.

serological refers to the properties of serum, particularly blood serum. The **serological response** is the production of antibodies in the blood serum in response to an infection.

signalled predictability refers to where a signal precedes an event and thus makes it predictable.

socialization a process whereby animals routinely interact with people and become familiar with them. A good simple definition is 'learning to get along with' people.

speciesism a term coined by Australian philosopher Peter Singer to mean the preferential consideration for human beings over non-human animals.

species survival plan (SSP) a captive breeding programme in North American zoos.

species-typical behaviours the repertoire of behaviours that characterize how a particular species behaves in the wild

spread of participation index (SPI) a technique that compares the observed frequency of use of different enclosure sectors with the frequency that we would expect, given their relative sizes, thus giving an index of the animal's use of the enclosure.

stereotypy a repetitive invariant behaviour, which may be the result of frustration, attempts to cope with a sub-optimal environment, or a dysfunction of the central nervous system.

sternal recumbancy a mammalian posture involving lying down with the sternum or breastbone on the ground, usually with the legs folded under the body, but with the body still in an upright position.

stimulus (pl. **stimuli**) a change in an animal's environment that may result in it changing its behaviour in an appropriate way. Stimuli can be features in the physical environment (such as light, temperature, sound, etc.), or in the internal environment (e.g. changes in hormone levels), or signals from other animals (e.g. postures, displays, pheromones).

stimulus enhancement a form of **learning** in which an animal learns an association as a result of having its attention drawn to the relevant **stimuli** by another animal.

stocking density the number of animals maintained in a particular area or volume of space.

stockmanship the skill of managing and caring for animals.

strength of motivation test a type of preference test in which it is assumed that an animal's willingness to 'work' for a resource reflects its level of motivation to gain the resource or to carry out the behaviour.

studbook a computerized database of all of the individual animals in a breeding programme for a given species (usually a threatened species). The aim of studbook management is to reduce inbreeding.

survival skills include the ability to orientate, avoid predators, and find suitable places to rest.

sustainability the long-term viability of ecosystems, or systems within agriculture, or forestry, or fishing, etc. The term is used to refer to systems that can continue at a set level indefinitely without collapsing. In 1987, the World Commission on Environment and Development developed the following definition (published in the Brundtland Report): '*Sustainable development meets the needs of the present without compromising the ability of future generations to meet their own needs*'.

symbiosis the close structural and physiological relationship between two or more species, which could not survive independently of the relationship.

T

taxon (pl. **taxa**)   any unit of **taxonomy** or classification, so the term can variously refer to a species, a genus, an order, or any other classification category.

Taxon Advisory Group (TAG)   a group comprising keepers, curators, **studbook** managers, etc. with specialist knowledge of a particular **taxon** (e.g. the penguin TAG, or the amphibian TAG). TAGs consider conservation issues, as well as husbandry. In the UK, such groups are referred to as Taxon Working Groups (TWGs).

taxonomy   the system of classifying plants and animals.

teleost   a bony fish (cf. **cartilaginous fish**; **elasmobranch**).

temporal predictability   refers to whether an event is provided at a fixed time (and thus is predictable), or at different times (so is unpredictable).

testiconid   a mammal in which the testes are located within the abdominal cavity rather than in a scrotal pouch (scrotum).

theory of mind   a theory that refers to an individual's knowledge of another individual's mental processes.

touch station   a place, particularly in aquariums, where visitors can come into close contact with animals.

trace element   element that is found in the body, often as part of an enzyme, and which appears to be necessary for metabolic function, but only in tiny amounts.

transmissible spongiform encephalopathies (TSEs)   diseases caused by **prions**, such as **bovine spongiform encephalopathy (BSE)** and **chronic wasting disease (CWD)**.

U

ultimate   *See* **functional**

ultrasonography   in relation to medicine, ultrasonography is diagnostic imaging technology that makes use of high-frequency sound waves or **ultrasound** to create an image of an internal part of the body.

ultrasound   the sound of a higher frequency than that which is detectable by the human ear and therefore above about 20 kHz (or 20,000 cycles per second).

ultraviolet (UV) light   light of very short wavelength, shorter than violet light, which is the shortest wavelength of light that the human eye is capable of seeing. The wavelength of UV light ranges from 400 **nanometres (nm)** down to 10nm. Most of the UV radiation that reaches the Earth's surface from the Sun is of wavelength 400–315nm, and is referred to as **UVA**.

ungulate   a term that refers to the members of the former taxonomic group Order Ungulata. The ungulates are the hoofed mammals, which are now grouped into a number of orders including the Order Perissodactyla (the odd-toed ungulates such as horses, tapirs, and rhinoceroses) and the Order Artiodactyla (the even-toed ungulates, such as cattle, deer, and giraffes).

utilitarian   a person who believes that the value of something depends on its utility (in other words, how useful it is), meaning that, for the utilitarian, some suffering by animals is justified if the benefit to humans outweighs the cost to the animals (e.g. the use of animal testing during the development of a cure for cancer).

utilitarianism   the idea that we should act so as to produce the greatest good (or utility) for the largest number of individuals.

V

vacuum activity   a behaviour that is carried out even if the appropriate **stimuli** are not present.

vector   in relation to disease, a vector is an organism which carries a pathogen from one animal to another (such as the mosquitos which transmit West Nile disease or avian malaria).

venepuncture   blood sampling, with a needle and syringe, from a vein.

viviparous   meaning giving birth to live young (cf. **oviparous**).

W

walk-through exhibit   an exhibit within which visitors and animals may not be separated by barriers.

wasting disease (or **wasting syndrome**)   illness as a result of which an animal shows progressive weight loss over a period of time.

welfare audit   a process of systematic review of animal records and husbandry parameters, with the aim

of identifying whether change is necessary to promote better welfare.

'willingness to pay' principle   a principle allowing consumers to promote animal welfare by making informed purchases and by paying more for animals farmed under 'improved' systems.

wing management   *See* **flight restraint**

Z

zoo   one definition of a zoo would be a collection of (mostly) wild animals, of different species, that is open to the public for a significant part of the year. Definitions of zoos vary widely, both in relation to national law and in common usage.

zoonosis (pl. **zoonoses**)   a disease that can be transmitted from non-human animals to humans.

Zootrition™   a nutritional software package and database.

Other useful glossaries

The glossary provided here is not exhaustive. For other useful glossaries, we recommend the following.

- **Glossary in Alcock (2009)** *Animal Behavior* The glossary at the end of this book is primarily to do with animal behaviour, but it covers some of the basic terms relating to mating systems and reproduction.

- **The National Human Genome Research Institute (NHGRI) 'Talking Glossary of Genetic Terms', available online at** http://www.genome.gov/10002096 A glossary designed to help those without scientific backgrounds to understand genetic research terms and concepts.

- **The Smithsonian National Zoological Park 'Great Apes & Other Primates' glossary, available online at** http://nationalzoo.si.edu/Animals/Primates/glossary.cfm (under the title 'Natural History explained')

References

A

AATA (Animal Transport Association) (2007) *AATA Manual for the Transportation of Live Animals* (2nd edn), Houston, TX: AATA.

AAZK (American Association of Zoo Keepers) (2004) *Enrichment Notebook* (CD-ROM format) (3rd edn), Topeka, KS: AAZK.

AAZK (American Association of Zoo Keepers) (2008) *Zoonotic Diseases* (CD-ROM format) (3rd edn), Topeka, KS: AAZK.

Abello, M. T., Colell, M., and Martin, M. (2007) 'Integration of one hand-reared cherry-crowned mangabey *Cercocebus torquatus torquatus* and two hand-reared drills *Mandrillus leucophaeus* into their respective family groups at Barcelona Zoo', *International Zoo Yearbook*, 41: 156–65.

Abeyesinghe, S. M., Nicol, C. J., Hartnell, S. J., and Wathes, C. M. (2005) 'Can domestic fowl, *Gallus gallus domesticus*, show self-control?', *Animal Behaviour*, 70: 1–11.

Adams, D. and Carwardine, M. (1991) *Last Chance to See*, London: Pan Books.

Addessi, E., Stammati, M., Sabbatini, G., and Visalberghi, E. (2005) 'How tufted capuchin monkeys (*Cebus apella*) rank monkey chow in relation to other foods', *Animal Welfare*, 14: 215–22.

Adelman, L. M., Falk, J. H., and James, S. (2000) 'Impact of National Aquarium in Baltimore on visitors' conservation attitudes, behavior and knowledge', *Curator*, 43: 33–61.

Adey, W. and Loveland, K. (2007) *Dynamic Aquaria: Building Living Ecosystems*, San Diego, CA: Academic Press.

Alcock, J. (2009) *Animal Behavior: An Evolutionary Approach* (9th edn), Sunderland, MA: Sinauer Associates.

Alford, P. L., Nash, L. T., Fritz, J., and Bowen, J. A. (1992). Effects of management practices on the timing of captive chimpanzee births. *Zoo Biology*, 11: 253–60.

Alford, P. L., Bloomsmith, M. A., Keeling, M. E., and Beck, T. F. (1995) 'Wounding aggression during the formation and maintenance of captive, multimale chimpanzee groups', *Zoo Biology*, 14: 347–59.

Allchurch, A. F. (2003) 'Yersiniosis in all taxa', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 724–7.

Allen, M. E. and Ullrey, D. E. (2004) 'Relationships among nutrition and reproduction and relevance for wild animals', *Zoo Biology*, 23: 475–87.

Almli, L. M. and Burghardt, G. M. (2006) 'Environmental enrichment alters the behavioral profile of ratsnakes (*Elaphe*)', *Journal of Applied Animal Welfare Science*, 9: 85–109.

Altman, J. D. (1998) 'Animal activity and visitor learning at the zoo', *Anthrozoös*, 11: 12–21.

Altmann, J. (1974) 'Observational study of behaviour: sampling methods', *Behaviour*, 49: 227–67.

Amato, G., Wharton, D., Zainuddin, Z. Z., and Powell, J. R. (1995) 'Assessment of conservation units for the Sumatran rhinoceros (*Dicerorhinus sumatrensis*)', *Zoo Biology*, 14: 395–402.

Ammerman, C. B. and Goodrich, R. D. (1983) 'Advances in mineral nutrition in ruminants', *Journal of Animal Science (Supplement)*, 57: 519–33.

Amosin, A., Payungporn, S., Theamboonlers, A., *et al.* (2006) 'Genetic characterization of H5N1 influenza A viruses isolated from zoo tigers in Thailand', *Virology*, 344: 480–91.

Andereck, K. L. and Caldwell, L. L. (1994) 'Variable selection in tourism market segmentation models', *Journal of Travel Research*, 33: 40–6.

Anderson, J. and Chamove, A. (1984) 'Allowing captive primates to forage', in Universities Federation for Animal Welfare (UFAW), *Standards in Laboratory Animal Management*, Wheathampsted: UFAW, pp. 253–356.

Anderson, J. R., Gillies, A., and Lock, L. C. (2010). *Pan* thanatology. *Current Biology*, 20: R349–51.

Anderson, U. S., Benne, M., Bloomsmith, M., and Maple, T. (2002) 'Retreat space and human visitor density moderate undesirable behaviour in petting zoo animals', *Journal of Applied Animal Welfare Science*, 5: 125–37.

Anderson, U. S., Kelling, A. S., Pressley-Keough, R., Bloomsmith, M. A., and Maple, T. L. (2003) 'Enhancing the zoo visitor's experience by public animal training and oral interpretation at an otter exhibit', *Environment and Behaviour*, 35: 826–41.

Anderson, U. S., Kelling, A. S., and Maple, T. L. (2008). Twenty-five years of *Zoo Biology*: a publication analysis. *Zoo Biology*, 27: 444–57.

Anziani, O., Zimmermann, G., Guglielmone, A., Forchieri, M., and Volpogni, M. (2000) 'Evaluation of insecticide ear tags containing ethion for control of pyrethroid-resistant *Haematobia irritans* (L.) on dairy cattle', *Veterinary Parasitology*, 91: 147–51.

Appleby, M. C. (1999) *What Should We Do About Animal Welfare?*, Oxford: Blackwell Science.

Appleby, M. C. and Hughes, B. O. (1997) *Animal Welfare*, Wallingford, Oxon: CABI Publishing.

Appleby, M. C., Hughes, B. O., Mench, J. A., and Olsson, A. (2011). *Animal Welfare.* Wallingford, Oxon.: CABI Publishing.

Arendt, J. and Skene, D. J. (2005) 'Melatonin as a chronobiotic', *Sleep Medicine Reviews*, 9: 25–39.

ARAZPA (Australasian Regional Association of Zoological Parks and Aquaria) (2008) *About ARAZPA*, available online at **http://www.arazpa.org.au/About-Us/default. aspx** (accessed April 2008).

Armstrong, S. (2004) 'A taste for grass: do zebra (*Equus burchelli*) have a preference for individual grass species?', in C. McDonald (ed.), *Proceedings of the Sixth Annual BIAZA Research Meeting*, 8–9 July, Edinburgh Zoo, Edinburgh, pp. 43–5.

Armstrong, S. and Botzler, R. (2003) *The Animal Ethics Reader*, London: Routledge.

Armstrong, S. and Marples, N. (2005) 'Do captive plains zebra (*E. burchelli*) have a preference for individual grass species?', in T. P. Meehan and M. E. Allen (eds), *Proceedings of the Fourth European Zoo Nutrition Conference*, Amsterdam: EAZA Executive Office.

Ari, C. and Correia, J. P. (2008) 'Role of sensory cues on food searching behaviour of a captive *Manta birostris* (Chondrichthyes, Mobulidae)', *Zoo Biology*, 27: 294–304.

Asa, C. S. (1996) 'Reproductive physiology', in D. G. Kleiman, M. Allen, K. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago Press, pp. 390–417.

Asa, C. S. and Porton, I. J. (2005) *Wildlife Contraception: Issues, Methods and Applications*, Baltimore, MD: Johns Hopkins University Press.

Ashley, P. J. (2007) 'Fish welfare: current issues in aquaculture', *Applied Animal Behaviour Science*, 104: 199–235.

Askue, L., Heimlich, J., Yu, J. P., Wang, X., and Lakley, S. (2009). Measuring a professional conservation education training program for zoos and wildlife parks in China. *Zoo Biology*, 28: 447–61.

Asvestas, C. and Reininger, M. (1999) 'Forming a bachelor group of long-tailed macaques (*Macaca fascicularis*)', *Laboratory Primate Newsletter*, 38: 14.

Atkinson, R. L., Atkinson, R. C., Smith, E. E., Bem, D. J., and Nolen-Hoeksema, S. (1996) *Hilgard's Introduction to Psychology* (12th edn), London: Harcourt Brace.

Aujard, F., Seguy, M., Terrien, J., Botalla, R., Blanc, S., and Perret, M. (2006) 'Behavioral thermoregulation in a non-human primate: effects of age and photoperiod on temperature selection', *Experimental Gerontology*, 41: 784–92.

Austin, M., Leader, L., and Reilly, N. (2005) 'Prenatal stress, the hypothalamic–pituitary–adrenal axis, and fetal and infant neurobehaviour', *Early Human Development*, 81: 917–26.

AZA (American Association of Zoos and Aquariums) (1999) *The Collective Impact of America's Zoos and Aquariums*, Silver Spring, MD: AZA.

AZA (American Association of Zoos and Aquariums) (2011) 'The Green Award', available online at **http://www.aza. org/Membership/detail.aspx?id=17624**.

AZA (American Association of Zoos and Aquariums) (2012) *Association of Zoos and Aquariums Species Survival Plan® (SSP) Program Handbook*, Silver Spring, MD: Association of Zoos and Aquariums.

B

Bach, C. (1998) *Birth Date Determination in Australasian Marsupials*, Taronga Zoo, Sydney: ARAZPA.

Baillie, J. M., Hilton-Taylor, C., and Stuart, S. N. (2004) *IUCN Red List of Threatened Species: A Global Species Assessment*, Gland, Switzerland: IUCN.

Baker, K. C. (1997) 'Straw and forage material ameliorate abnormal behaviour in adult chimpanzees', *Zoo Biology*, 16: 225–36.

Baker, K. C. (2000) 'Advanced age influences chimpanzee behavior in small social groups', *Zoo Biology*, 19: 111–19.

Baker, K. C. (2004) 'Benefits of positive human interaction for socially housed chimpanzees', *Animal Welfare*, 13: 239–45.

Balke, J. M. E., Barker, I. K., Hackenberger, M. K., McManamon, R., and Boever, W. J. (1988) 'Reproductive anatomy of three nulliparous female Asian elephants: the development of artificial breeding techniques', *Zoo Biology*, 7: 99–113.

Ballou, J. D., Lacy, R. C., and Pollak, J. P. (2011) *PMx: software for demographic and genetic analysis and management of pedigreed populations (version 1.0)*, Brookfield, IL: Chicago Zoological Society.

Balmford, A. (2000) 'Separating fact from artefact in analyses of zoo visitor preferences', *Conservation Biology*, 14: 1193–5.

Balmford, A., Leader-Williams, N., and Green, M. J. B. (1995) 'Parks or arks: where to preserve threatened mammals?', *Biodiversity and Conservation*, 4: 595–607.

Balmford, A., Mace, G. M., and Leader-Williams, N. (1996) 'Designing the ark: setting priorities for captive breeding', *Conservation Biology*, 10: 719–27.

Balmford, A., Leader-Williams, N., Mace, G. M., *et al.* (2007) 'Message received? Quantifying the impact of informal conservation education on adults visiting UK zoos', in A. Zimmermann, M. Hatchwell, L. Dickie, and C. West (eds), *Zoos in the 21st Century: Catalysts for Conservation?*, Cambridge: Cambridge University Press, pp. 120–36.

Baratay, E. and Hardouin-Fugier, E. (2004) *Zoo: A History of Zoological Gardens in the West*, London: Reaktion Books.

Barber, J., Lewis, D., Govindasamy, A., and Stevenson, M. F. (2010). 'Setting standards for evaluation of captive facilities', in D. G. Kleiman, K. V. Thompson and C. Kirk Baer (eds), *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: University of Chicago Press, pp. 22–34.

Barbosa, A. (2009). 'The role of zoos and aquariums in research into the effects of climate change on animal health', *International Zoo Yearbook*, 43: 131–5.

Barker, D., Fitzpatrick, M. P., and Dierenfeld, E. S. (1998) 'Nutrient composition of selected whole invertebrates', *Zoo Biology*, 17: 123–34.

Barnard, C. and Hurst, J. (1996) 'Welfare by design: the natural selection of welfare criteria', *Animal Welfare*, 56: 405–33.

Barnard, C., Gilbert, F., and McGregor, P. (1993) *Asking Questions in Biology: Design, Analysis and Presentation in Practical Work*, Upper Saddle River, NJ: Prentice Hall.

Barr, S., Laming, P. R., Dick, J. T. A., and Elwood, R. W. (2008) 'Nociception or pain in a decapod crustacean?', *Animal Behaviour*, 75: 745–51.

Barrington-Johnson, J. (2005) *The Zoo: The Story of London Zoo*, London: Robert Hale.

Bartlett, A. D. (1890) *Life Among Wild Beasts in the Zoo*, London: Chapman & Hall.

Bartlett, A. D. (1898) *Wild Animals in Captivity*, London: Chapman & Hall.

Bashaw, M. (2011) 'Consistency of captive giraffe behavior under two different management regimes', *Zoo Biology* 30: 371–8.

Bashaw, M. J. and Maple, T. L. (2001) 'Signs fail to increase zoo visitors' ability to see tigers', *Curator*, 44: 297–304.

Bashaw, M. J., Tarou, L. R., Maki, T. S., and Maple, T. L. (2001) 'A survey assessment of variables related to stereotypy in captive giraffe and okapi', *Applied Animal Behaviour Science*, 73: 235–47.

Bashaw, M. J., Bloomsmith, M. A., Marr, M. J., and Maple, T. L. (2003) 'To hunt or not to hunt? A feeding enrichment experiment with captive large felids', *Zoo Biology*, 22: 189–98.

Bashaw, M. J., Kelling, A. S., Bloomsmith, M. A., and Maple, T. L. (2007) 'Environmental effects on the behavior of zoo-housed lions and tigers, with a case study of the effects of a visual barrier on pacing', *Journal of Applied Animal Welfare Science*, 10: 95–109.

Bassett, L. and Buchanan-Smith, H. M. (2007) 'Effects of predictability on the welfare of captive animals', *Applied Animal Behaviour Science, Conservation, Enrichment and Animal Behaviour*, 102: 223–45.

Bassett, L., Buchanan-Smith, H. M., McKinley, J., and Smith, T. E. (2003) 'Effects of training on stress-related behaviour of the common marmoset (*Callithrix jacchus*) in relation to coping with routine husbandry procedures', *Journal of Applied Animal Welfare Science*, 6: 221–33.

Bateson, P. and Bradshaw, E. (1997) 'Physiological effects of hunting red deer (*Cervus elaphus*)', *Proceedings of the Royal Society (Series B: Biological Sciences)*, 264: 1707–14.

Batzina, A. and Karakatouli, N. (2012) 'The presence of substrate as a means of environmental enrichment in intensively reared gilthead seabream *Sparus aurata*: growth and behavioral effects', *Aquaculture*, 370–1: 54–60.

Bauert, M. R., Furrer, S. C., Zingg, R., and Steinmetz, H. W. (2007) 'Three years of experience running the Masoala Rainforest ecosystem at Zurich Zoo, Switzerland', *International Zoo Yearbook*, 41: 203–16.

Baxter, E. and Plowman, A. B. (2001) 'The effect of increasing dietary fibre on feeding, rumination and oral stereotypies in captive giraffes (*Giraffa camelopardalis*)', *Animal Welfare*, 10: 281–90.

Bayley, J. E., Yu, M., and Frediani, K. (2010). 'Sustainable food production using high density vertical growing (Verticrop)', *ISHS Acta Horticulturae 921:International Symposium on Horticulture for Development*, available online at **http://www.actahort. org/members/showpdf?booknrarnr=921_11**.

Beardsworth, A. and Bryman, A. E. (2001) 'The wild animal in late modernity: the case of the Disneyization of zoos', *Tourist Studies*, 1: 83–104.

Beausoleil, N. J., Mellor, D. J., and Stafford, K. J. (2004) *Methods for Marking New Zealand Wildlife: Amphibians, Reptiles and Marine Mammals*, Wellington: DOC Science Publishing.

Beck, B. B., Rapaport, L. G., Stanley-Price, M. R., and Wilson, A. C. (1994) 'Reintroduction of captive born animals', in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner (eds), *Creative Conservation: Interactive Management of Wild and Captive Animals*, London: Chapman & Hall, pp. 265–86.

Becker, P. A., Miller, P. S., Gunther, M. S., Somers, M. J., Wildt, D. E., and Maldonado, J. E. (2012) Inbreeding avoidance influences the viability of reintroduced populations of African wild dogs (*Lycaon pictus*). *PLoS One*, 7 (Special Issue 1): e37181.

Bekoff, M. and Byers, J. (1998) *Animal Play: Evolutionary, Comparative and Ecological Perspectives*, Cambridge: Cambridge University Press.

Bell, C. E. (ed.) (2001) *Encyclopedia of the World's Zoos*, Chicago, IL/London: Fitzroy Dearborn.

Benesch, A. R., Munro, U., Krop, T., and Fleissner, G. (2010). Seasonal changes in the behaviour and circadian rhythms in activity and behaviour of captive koalas *Phascolarctos cinereus*. *Biological Rhythm Research*, 41: 289–304.

Bengis, R. G. (2012) 'Anthrax in free-ranging wildlife', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Elsevier Saunders, pp. 98–107.

Benirschke, K., Kumamoto, A. T., and Bogart, M. H. (1981) 'Congenital anomalies in *Lemur variegatus*', *Journal of Medical Primatology*, 10: 38–45.

Bennett, P. (2001) 'Establishing animal germplasm resource banks for wildlife conservation: genetic, population and evolutionary aspects', in P. Watson and W. Holt (eds), *Cryobanking the Genetic Resource: Wildlife Conservation for the Future?*, London: Taylor & Francis, pp. 47–67.

Berg, J. K. (1983) 'Vocalizations and associated behaviours of the African elephant (*Loxodonta africana*) in captivity', *Zeitschrift für Tierpsychologie*, 63: 63–79.

Berge, G. M. (1990) 'Freeze branding of Atlantic halibut', *Aquaculture*, 89: 383–6.

Bergeron, R., Badnell-Waters, A., Lambton, S., and Mason, G. (2006) 'Stereotypic oral behaviour in captive ungulates: foraging, diet and gastrointestinal function', in G. J. Mason (ed.), *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*, Wallingford, Oxon: CABI Publishing, pp. 19–57.

Berkson, G., Mason, W., and Saxon, S. (1963) 'Situation and stimulus effect on stereotyped behaviours of chimpanzees', *Journal of Comparative Physiological Psychology*, 56: 786–92.

Bernard, J. B. (1997) *Vitamin D and Ultraviolet Radiation: Meeting Lighting Needs for Captive Animals*, EAZA Nutrition Advisory Group (NAG) Fact Sheet 002 (July 1997), available online at **http://www. nagonline.net/Technical%20Papers/NAGFS00297VitD-JONIFEB24,2002MODIFIED.pdf**.

Bernard, J. B., Watkins, B., and Ullrey, D. (1989) 'Manifestations of vitamin D deficiency in chicks reared under different artificial lighting regimes', *Zoo Biology*, 8: 349–55.

Bernstein, I. S. (1967) 'Defining the natural habitat', in D. Starck, R. Schneider, and H.-J. Kuhn (eds), *Progress in Primatology*, Stuttgart: Fischer, pp. 177–9.

Bertolino, S., Viano, C., and Currado, I. (2001) 'Population dynamics, breeding patterns and spatial use of the garden dormouse (*Eliomys quercinus*) in an Alpine habitat', *Journal of Zoology*, 253: 513–21.

Bertram, B. (2004) 'Misconceptions about zoos', *Biologist*, 51: 199–206.

Besag, J. and Clifford, P. (1989) 'Generalized Monte Carlo significance tests', *Biometrika*, 76: 633–42.

Bestelmeyer, S. V. (1999) 'Behavioural changes associated with introductions of male maned wolves (*Chrysocyon brachyurus*) to females with pups', *Zoo Biology*, 18: 189–97.

BIAZA (British and Irish Association of Zoos and Aquariums) (2007) *Working Together for Wildlife*, London: BIAZA.

BIAZA (British and Irish Association of Zoos and Aquariums) (2010a) *An Economic Impact Assessment for the Zoo and Aquarium Sector*, London. BIAZA, available at **http:www.biaza.org.uk/publications/other-publications/**

BIAZA (British and Irish Association of Zoos and Aquariums) (2010b). *Management Guidelines for the Welfare of Zoo Animals: Elephants* (3rd edn), BIAZA, London.

Birke, L. (2002) 'Effects of browse, human visitors and noise on the behaviour of captive orang-utans', *Animal Welfare*, 11: 189–202.

Birkett, L. P. and Newton-Fisher, N. E. (2011). 'How abnormal is the behaviour of captive, zoo-living chimpanzees?' *PLoS One* 6: e20101.

Biro, P. A. and Stamps, J. A. (2008) 'Are animal personality traits linked to life-history productivity?' *Trends in Ecology and Evolution,* 23: 361–86.

Bitgood, S. (2002) 'Environmental psychology in museums, zoos and other exhibition centres', in R. B. Bechtel and A. Churchman (eds), *Handbook of Environmental Psychology*, New York: John Wiley, pp. 461–80.

Bitgood, S., Patterson, D., and Benefield, A. (1988) 'Exhibit design and visitor behavior: empirical relationships', *Environment and Behavior*, 20: 474–91.

Blaney, E. C. and Wells, D. L. (2004) 'The influence of a camouflage net barrier on the behaviour, welfare and public perceptions of zoo-housed gorillas', *Animal Welfare*, 13: 111–18.

Blasetti, A., Boltani, L., Riviello, M. C., and Visalberghi, E. (1988) 'Activity budgets and use of enclosed space by wild boars (*Sus scrofa*) in captivity', *Zoo Biology*, 7: 69–79.

Blomqvist, L. (1995) 'Three decades of snow leopards *Panthera uncia* in captivity', *International Zoo Yearbook*, 34: 178–85.

Bloomsmith, M. A. and Lambeth, S. P. (1995) 'Effects of predictable versus unpredictable feeding schedules on chimpanzee behavior', *Applied Animal Behaviour Science*, 44: 65–74.

Bloomsmith, M. A. and Lambeth, S. P. (2000) 'Videotapes as enrichment for captive chimpanzees (*Pan troglodytes*)', *Zoo Biology*, 19: 541–51.

Bloomsmith, M. A., Laule, G. E., Alford, P. L., and Thurston, R. H. (1994) 'Using training to moderate chimpanzee aggression during feeding', *Zoo Biology*, 13: 557–66.

Bloomsmith, M. A., Stone, A. M., and Laule, G. E. (1998) 'Positive reinforcement training to enhance the voluntary movement of group-housed chimpanzees within their enclosures', *Zoo Biology*, 17: 333–41.

Bloomsmith, M. A., Jones, M. L., Snyder, R. J., *et al.* (2003) 'Positive reinforcement training to elicit voluntary movement of two giant pandas throughout their enclosure', *Zoo Biology*, 22: 323–34.

Bloomsmith, M. A., Marr, M. J., and Maple, T. L. (2007) 'Addressing non-human primate behavioral problems through the application of operant conditioning: is the human treatment approach a useful model?', *Applied Animal Behaviour Science*, 102: 205–22.

Bloxam, Q. M. C. and Tonge, S. J. (1995) 'Amphibians: suitable candidates for breeding-release programmes', *Biodiversity and Conservation*, 4: 636–44.

Blunt, W. (1976) *The Ark in the Park: The Zoo in the Nineteenth Century*, London: Hamish Hamilton.

Boakes, E. H., Wang, J., and Amos, W. (2006) 'An investigation of inbreeding depression and purging in captive pedigreed populations', *Heredity*, 98: 172–82.

Boehm, T. and Zufall, F. (2006) 'MHC peptides and the sensory evaluation of genotype', *Trends in Neurosciences*, 29: 100–7.

Boinski, S. (1987) 'Mating patterns in squirrel monkeys (*Saimiri oerstedi*)', *Behavioral Ecology and Sociobiology*, 21: 13–21.

Boinski, S., Gross, T. S., and Davis, J. K. (1999) 'Terrestrial predator alarm vocalizations are a valid monitor of stress in captive brown capuchins (*Cebus apella*)', *Zoo Biology*, 18: 295–312.

Boissy A., Manteuffel, G., Jensen, M. B., *et al.* (2007) 'Assessment of positive emotions in animals to improve their welfare', *Physiology and Behavior*, 92: 375–97.

Boivin, X., Garel, J. P., Mante, A., and Le Neindre, P. (1998) 'Beef calves react differently to different handlers according to the test situation and their previous interactions with their caretaker', *Applied Animal Behaviour Science*, 55: 245–57.

Boivin, X., Lensink, J., Tallet, C., and Veissier, I. (2003) 'Stockmanship and farm animal welfare', *Animal Welfare*, 12: 479–92.

Bolin, C. A. (2003) 'Leptospirosis', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Elsevier Saunders, pp. 699–702.

Bond, J. C. and Lindburg, D. G. (1990) 'Carcass feeding of captive cheetahs (*Acinonyx jubatus*): the effects of a naturalistic breeding program on oral health and psychological well-being', *Applied Animal Behaviour Science*, 26: 373–82.

Boness, D. (1996) 'Water quality management in aquatic mammal exhibits', in D. Kleiman, M. Allen, K. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago Press, pp. 231–42.

Boogaard, B. K., Oosting, S. J., and Bock, B. B. (2006) 'Elements of societal perception of farm animal welfare: a quantitative study in the Netherlands', *Livestock Science*, 104: 13–22.

Boorer, M. (1972) 'Some aspects of stereotyped patterns of movement exhibited by zoo animals', *International Zoo Yearbook*, 12: 164–8.

Bostock, S. St. C. (1993) *Zoos and Animal Rights*, London: Routledge.

Bottrill, M. C., Joseph, L. N., Carwardine, J., *et al.* (2008) 'Is conservation triage just smart decision making?', *Trends in Ecology and Evolution*, 23: 649–54.

Bowden, C. and Masters, J. (2003) *Textbook of Veterinary Medical Nursing*, Oxford: Butterworth Heinemann.

Bowers, B. B. and Burghardt, G. M. (1992) 'The scientist and the snake: relationships with reptiles', in H. Davis and D. Balfour (eds), *The Inevitable Bond: Examining Scientist–Animal Interactions*, Cambridge: Cambridge University Press, pp. 250–63.

Bowkett, A. E. (2009). 'Recent captive-breeding proposals and the return of the ark concept to global species conservation', *Conservation Biology*, 23: 773–6.

Bowkett, A. E., Plowman, A. B., Stevens, J. R., Davenport, T. R. B., and Jansen van Vuuren, B. (2009) 'Genetic testing of dung identification for antelope surveys in Udzungwa Mountains, Tanzania' *Conservation Genetics*, 10: 251–5.

Bowler, M. T., Buchanan-Smith, H., and Whiten, A. (2012) 'Assessing public engagement with science in a university primate research centre in a national zoo', *PLoS One*, 7: e34505.

Box, H. (1991) 'Training for life after release: simian primates as examples', *Symposium of the Zoological Society of London*, 62: 111–23.

Braithwaite, V. A., and Huntingford, F. A. (2004) 'Fish and welfare: do fish have the capacity for pain perception and suffering?', *Animal Welfare*, 13: 581–92.

Braswell, L. D. (1991) 'Exotic animal dentistry', *Compendium on Continuing Education for the Practicing Veterinarian*, 13: 1229–33.

Bredin, I. P., Skinner, J. D., and Mitchell, G. (2008). Can osteophagia provide giraffes with phosphorus and calcium? *Onderstepoort Journal of Veterinary Research*, 75: 1–9.

Bremner-Harrison, S., Prodohl, P. A., and Elwood, R. (2004) 'Behavioural trait assessment as a release criterion: boldness predicts early death in a reintroduction programme of captive-bred swift fox (*Vulpes velox*)', *Animal Conservation*, 7: 313–20.

Brent, L. and Stone, A. M. (1996) 'Long-term use of televisions, balls, and mirrors as enrichment for paired and singly caged chimpanzees', *American Journal of Primatology*, 39: 139–45.

Brent, L., Kessel, A. L., and Barrera, H. (1997) 'Evaluation of introduction procedures in captive chimpanzees', *Zoo Biology*, 16: 335–42.

Briffa, M. and Weiss, A. (2010). 'Animal personality', *Current Biology*, 20: R912.

Briffa, M. and Twyman, C. (2011). 'Do I stand out or blend in? Conspicuousness awareness and consistent behavioural differences in hermit crabs', *Biology Letters*, 7: 311–32.

Britt, A. (1998) 'Encouraging natural feeding behaviour in captive bred black and white ruffed lemurs (*Varecia variegata v.*)', *Zoo Biology*, 17: 379–92.

Broad, G. (1996) 'Visitor profile and evaluation of informal education at Jersey Zoo', *Dodo: Journal of the Jersey Wildlife Preservation Trust*, 32: 166–92.

Brodey, P. (1981) 'The LINKS-ZOO: a recreational/educational facility for the future', *International Zoo Yearbook*, 21: 63–8.

Broom, D. M. (1998) 'Stereotypies in animals', in M. Bekoff and C. A. Meaney (eds), *Encyclopedia of Animal Rights and Animal Welfare*, Chicago, IL/London: Fitzroy Dearborn, p. 256.

Broom, D. M. (2005) 'The effects of land transport on animal welfare', *Revue Scientifique et Technique de l'Office International des Epizooties*, 24: 683–91.

Broom, D. M. and Johnson, K. G. (1993) *Stress and Animal Welfare*, London: Chapman & Hall.

Brooman, S. and Legge, D. (1997) *Law Relating to Animals*, London: Cavendish Publishing.

Brown, C. and Loskutoff, N. (1998) 'A training program for non-invasive semen collection in captive western lowland gorillas (*Gorilla gorilla gorilla*)', *Zoo Biology*, 17: 143–51.

Brown, J. L. (2000) 'Reproductive endocrine monitoring of elephants: an essential tool for assisting captive management', *Zoo Biology*, 19: 347–69.

Brown, J. L. and Wemmer, C. M. (1995) 'Urinary cortisol analysis for monitoring adrenal activity in elephants', *Zoo Biology*, 14: 533–42.

Brown, J. L., Olson, D., Keele, M., and Freeman, E. W. (2004) 'Survey of the reproductive cyclicity status of Asian and African elephants in North America', *Zoo Biology*, 23: 309–21.

Brummer, S. P., Gese, E. M., and Shivik, J. A. (2010). 'The effect of enclosure type on the behaviour and heart rate of captive coyotes,' *Applied Animal Behaviour Science*, 125: 171–80.

Brydges, N. M., Leach, M., Nicol, K., Wright, R., and Bateson, M. (2011) 'Environmental enrichment induces optimistic cognitive bias in rats', *Animal Behaviour*, 81: 169–75.

Bubier, N. (1996) 'The behavioural priorities of laying hens: the effects of two methods of environmental enrichment on time budgets', *Behavioural Processes*, 374: 239–49.

Buchanan-Smith, H. M., Anderson, D. A., and Ryan, C. W. (1993) 'Responses of cotton-top tamarins (*Saguinus oedipus*) to faecal scents of predators and non-predators', *Animal Welfare*, 2: 17–32.

Buckanoff, H., Frederick, C., and Weston Murphy, H. (2006) 'Hand-rearing a potto *Perodicticus potto* at Franklin Park Zoo, Boston', *International Zoo Yearbook*, 40: 302–12.

Burghardt, G. M. (1995) 'Brain imaging, ethology and the non-human mind', *Behavioural and Brain Sciences*, 18: 339–40.

Burghardt, G. M., Ward, B., and Rosscoe, R. (1996) 'Problem of reptile play: environmental enrichment and play behavior in a captive Nile soft-shelled turtle, *Trionyx triunguis*', *Zoo Biology*, 15: 223–38.

Burke, T. and Bruford, M. W. (1987) 'DNA fingerprinting in birds', *Nature*, 327: 149–52.

Burkhardt, R. W. (2001) 'A man and his menagerie: management of a nineteenth-century zoological park by Frédéric Cuvier', *Natural History*, 110: 62–9.

Burley, N. (1985) 'Leg-band color and mortality patterns in captive breeding populations of zebra finches', *Auk*, 102: 647–51.

Burman, O. H. P., Ilyat, A., Jones, G., and Mendl, M. (2007) 'Ultrasonic vocalizations as indicators of welfare for laboratory rats (*Rattus norvegicus*)', *Applied Animal Behaviour Science*, 10: 116–29.

Burman, O., Parker, R., Paul, E., and Mendl, M. (2008) 'A spatial judgement task to determine background emotional state in laboratory rats *(Rattus norvegicus)*' *Animal Behaviour*, 76: 801–9.

Bush, M. (1993) 'Anaesthesia of high-risk animals: giraffe', in M. E. Fowler (ed.), *Zoo and Wild Animal Medicine* (3rd edn), Philadelphia, PA: W. B. Saunders.

Bush, M. (2003) '*Giraffidae*', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier.

Bush, M., Montali, R. J., Brownstein, D., James, A. E., and Appel, M. J. G. (1976) 'Vaccine-induced canine distemper in a lesser panda', *Journal of the American Veterinary Medical Association*, 169: 959–60.

Bustamante, J. (1996). Population viability analysis of captive and released bearded vulture populations. *Conservation Biology*, 10: 822–31.

Byford, R. L., Craig, M. E., and Crosby, B. L. (1992) 'A review of ectoparasites and their effect on cattle production', *Journal of Animal Science*, 70: 597–602.

C

Cain, L. and Meritt, D., Jr (2008). 'The demand for zoos and aquariums', *Tourism Review International*, 11: 295–306.

Caine, J. and Melfi, V. (2005) 'A long term study of *Trichuris trichiura* in zoo-housed colobus', in A. Nicklin (ed.), *Proceedings of the Seventh Annual Symposium on Zoo Research*, London: BIAZA, pp. 56–66.

Caine, N. G. and O'Boyle, V. J. Jr (1992) 'Cage design and forms of play in red-bellied tamarins, *Saguinus labiatus*', *Zoo Biology*, 11: 215–20.

Calle, P. P. (2003) 'Rabies', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 732–6.

Canfield, P. J. and Cunningham, A. A. (1993) 'Disease and mortality in Australian marsupials held at London Zoo, 1872–1972', *Journal of Zoo and Wildlife Medicine*, 24: 158–67.

Canino, W. and Powell, D. (2009). 'Formal behavioural evaluation of enrichment programs on a zookeeper's schedule: a case study with a polar bear (*Ursus maritimus*) at the Bronx Zoo', *Zoo Biology*, 29: 503–8.

Capitanio, J. P. (1999) 'Personality dimensions in adult male rhesus macaques: prediction of behaviors across time and situation', *American Journal of Primatology*, 47: 299–320.

Carcopino, J. (1991) *Daily Life in Ancient Rome: The People and the City at the Height of the Empire*, Harmondsworth: Penguin.

Cardillo, M., Mace, G. M., Jones, K. E., *et al.* (2005) 'Multiple causes of high extinction risk in large mammal species', *Science*, 309: 1239–41.

Carlson, N. (2007) *Physiology of Behaviour*, Boston, MA: Pearson Education.

Carlstead, K. (1996) 'Effects of captivity on the behavior of wild mammals', in D. G. Kleiman, M. Allen, K. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago Press, pp. 317–33.

Carlstead, K. (1998) 'Determining the causes of stereotypic behaviors in zoo carnivores: towards appropriate enrichment strategies', in D. Shepherdson, J. Mellen, and M. Hutchins (eds), *Second Nature: Environmental Enrichment for Captive Animals*, Washington, DC: Smithsonian Institute Press, pp. 172–83.

Carlstead, K. (2009). 'A comparative approach to the study of keeper–animal relationships in the zoo', *Zoo Biology*, 28: 589–608.

Carlstead, K. and Brown, J. L. (2005) 'Relationships between patterns of fecal corticoid excretion and behavior, reproduction, and environmental factors in captive black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros', *Zoo Biology*, 24: 215–32.

Carlstead, K. and Seidensticker, J. (1991) 'Seasonal variation in stereotypic pacing in an American black bear *Ursus americanus*', *Behavioural Processes*, 25: 155–61.

Carlstead, K. and Shepherdson, D. (1994) 'Effects of environmental enrichment on reproduction', *Zoo Biology*, 13: 447–58.

Carlstead, K., Seidensticker, J., and Baldwin, R. (1991) 'Environmental enrichment for zoo bears', *Zoo Biology*, 10: 3–16.

Carlstead, K., Brown, J. L., and Seidensticker, J. (1993) 'Behavioral and adrenocortical responses to environmental changes in leopard cats (*Felis bengalensis*)', *Zoo Biology*, 12: 321–31.

Carlstead, K., Mellen, J., and Kleiman, D. G. (1999a) 'Black rhinoceros (*Diceros bicornis*) in US zoos. I:

Individual behaviour profiles and their relationship to breeding success', *Zoo Biology*, 18: 17–34.

Carlstead, K., Fraser, J., Bennett, C., and Kleiman, D. G. (1999b) 'Black rhinoceros (*Diceros bicornis*) in US zoos. II: Behavior, breeding success, and mortality in relation to housing facilities', *Zoo Biology*, 18: 35–52.

Caro, T. M. (1993) 'Behavioral solutions to breeding cheetahs in captivity: insights from the wild', *Zoo Biology*, 12: 19–30.

Carr, N. and Cohen, S. (2011) 'The public face of zoos: images of entertainment, education and conservation', *Anthrozoös*, 24: 175–89.

Carrasco, L., Colell, M., Calvo, M., Abello, M. T., Velasco, M., and Posada, S. (2009) 'Benefits of training/playing therapy in a group of captive lowland gorillas (*Gorilla gorilla gorilla*)', *Animal Welfare*, 18: 9–19.

Carson, R. (1951) *The Sea Around Us*, New York: Oxford University Press.

Carwardine, M. (2009) *Last Chance to See*, London: HarperCollins.

Castellote, M. and Fossa, F. (2006) 'Measuring acoustic activity as a method to evaluate welfare in captive beluga whales (*Delphinapterus leucas*)', *Aquatic Mammals*, 32: 325–33.

Cavalieri, P. and Singer, P. (eds) (1994) *The Great Ape Project: Equality Beyond Humanity*, New York: St Martin's Griffin.

Cavigelli, S. A., Yee, J. R., and McClintock, M. K. (2006) 'Infant temperament predicts life span in female rats that develop spontaneous tumors', *Hormones and Behavior*, 50: 454–62.

Caws, C. and Aureli, F. (2003) 'Chimpanzees cope with temporary reduction of escape opportunities', *International Journal of Primatology*, 24: 1077–91.

CBSG (Conservation Breeding Specialist Group) of the World Conservation Union (IUCN) (2004) 'Transponders', *CBSG News*, 15: 20.

Ceballos, G., Erhlich, P. R., Soberón, J., Salazar, I., and Fay, J. P. (2005) 'Global mammal conservation: what must we manage?', *Science*, 309: 603–7.

Central Zoo Authority (2009). *Zoos in India: Legislation, Policy, Guidelines and Strategies*. New Delhi: Central Zoo Authority.

Cerit, H. and Avanus, K. (2007) 'Sex identification in avian species using DNA typing methods', *World's Poultry Science Journal*, 63: 91–9.

Chai, N. (2012) 'Mycobacteriosis in amphibians', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 224–30.

Chalmers, K. (2006) *Zoo Keeper Information: Auckland Zoo and its Role in Conservation and Captive Breeding Programmes*, Auckland, NZ: Auckland Zoo.

Chamove, A. (1988) 'Assessing the welfare of captive primates: a critique', in Universities Federation for Animal Welfare (UFAW), *Symposium of Laboratory Animal Welfare Research: Primates*, Potters Bar, Herts: UFAW, pp. 39–49.

Chamove, A. (1989) 'Environmental enrichment: a review', *Animal Technology*, 40: 155–78.

Chamove, A. and Moodie, E. (1990) 'Are alarming events good for captive monkeys?', *Applied Animal Behaviour Science*, 276: 169–76.

Chamove, A. and Rohrhuber, B. (1989) 'Moving callitrichid monkeys from cages to outside areas', *Zoo Biology*, 8: 151–63.

Chamove, A., Anderson, J., Morgan-Jones, S., and Jones, S. (1982) 'Deep woodchip litter: hygiene, feeding, and behavioural enhancement in eight primate species', *International Journal for the Study of Animal Problems*, 3: 308–18.

Chamove, A. S., Hosey, G. R., and Schaetzel, P. (1988) 'Visitors excite primates in zoos', *Zoo Biology*, 7: 359–69.

Chandroo, K. P., Duncan, I. J. H., and Moccia, R. D. (2004) 'Can fish suffer? Perspectives on sentience, pain, fear and stress', *Applied Animal Behaviour Science*, 86: 225–50.

Chang, T. R., Forthman, D. L., and Maple, T. L. (1999) 'Comparison of confined mandrill (*Mandrillus sphinx*) behaviour in traditional and "ecologically representative" exhibits', *Zoo Biology*, 18: 163–76.

Charlton, B. D., Keating, J. L., Kersey, D., Rengui, L., Huang, Y., and Swaisgood, R. R. (2011). Vocal cues to male androgen levels in giant pandas. *Biology Letters*, 7: 71–4.

Chastain, B. (2005) 'The defining moment', in *Innovation or Replication: Proceedings of the Sixth International Symposium on Zoo Design*, Paignton, Devon: Whitley Wildlife Conservation Trust.

Cheek, N. (1976) 'Sociological perspectives on the zoological park market', in N. H. Cheek, D. R. Field, and R. J. Burge (eds), *Leisure and Recreation Places*, Ann Arbor, MI: Ann Arbor Science.

Chelluri, G. I., Ross, S. R., and Wagner, K. E. (2013) 'Behavioral correlates and welfare implications of informal interactions between caretakers and zoo-housed chimpanzees and gorillas', *Applied Animal Behaviour Science*, in press.

Cherfas, J. (1984) *Zoo 2000: A Look Beyond the Bars*, London: BBC.

Choo, Y., Todd, P. A., and Li, D. (2011). 'Visitor effects on zoo orang-utans in two novel, naturalistic enclosures', *Applied Animal Behaviour Science*, 133: 78–86.

Cirulli, F., Berry, A., and Alleva, E. (2003) 'Early disruption of the mother–infant relationship: effects on brain plasticity and implications for psychopathology', *Neuroscience and Biobehavioral Reviews*, 27: 73–82.

Clark, F. E. (2011a) 'Space to choose: network analysis of social preferences in a captive chimpanzee community, and implications for management', *American Journal of Primatology*, 73: 748–57.

Clark, F. E. (2011b) 'Great ape cognition and care: can cognitive challenges enhance psychological well-being?' *Applied Animal Behaviour Science,* 35: 1–12.

Clark, F. E. and King, A. (2008) 'A critical review of zoo-based olfactory enrichment', in J. Hurst, R. Beynon, S. Roberts, and T. Wyatt (eds), *Chemical Signals in Vertebrates 11*, New York: Springer, pp. 391–8.

Clark, F. E. and Melfi, V. A. (2012) 'Environmental enrichment for a mixed-species nocturnal mammal exhibit', *Zoo Biology*, 31: 397–413.

Clauss, M. and Dierenfeld, E. S. (2007) 'The nutrition of "browsers"', in M. E. Fowler and R. E. Miller, *Zoo and Wild Animal Medicine: Current Therapy* (6th edn), Philadelphia, PA: Saunders Elsevier, pp. 444–54.

Clauss, M., and Fidgett, A. (eds) (2009) *Zoo Animal Nutrition* (Vol. IV), Fürth, Germany: Filander Verlag.

Clauss, M. and Hatt, J.-M. (2006) 'The feeding of rhinoceros in captivity', *International Zoo Yearbook*, 40: 197–209.

Clauss, M., Kienzle, E., and Wiesner, H. (2003) 'Feeding browse to large zoo herbivores: how much is "a lot", how much is "sufficient"?', in A. Fidgett, M. Clauss, U. Ganslosser, J.-M. Hatt, and J. Niijboer (eds), *Zoo Animal Nutrition* (Vol. II), Fürth, Germany: Filander Verlag, pp. 17–25.

Clauss, M., Polster, C., Kienzle, E., *et al.* (2005) 'Energy and mineral nutrition and water intake in the captive Indian rhinoceros (*Rhinoceros unicornis*)', *Zoo Biology*, 24: 1–14.

Claxton, A. M. (2011) 'The potential of the human–animal relationship as an environmental enrichment for the welfare of zoo-housed animals', *Applied Animal Behaviour Science*, 133: 1–10.

Clayton, S., Fraser, J., and Saunders, C. D. (2009) 'Zoo experiences: conversations, connections, and concern for animals', *Zoo Biology*, 28: 377–97.

Clubb, R. and Mason, G. (2002) *A Review of the Welfare of Zoo Elephants in Europe*, Oxford: Animal Behaviour Research Group, University of Oxford.

Clubb, R. and Mason, G. (2003) 'Captivity effects on wide-ranging carnivores', *Nature*, 425: 473–4.

Clubb, R. and Mason, G. (2004) 'Pacing polar bears and stoical sheep: testing ecological and evolutionary hypotheses about animal welfare', *Animal Welfare*, 13: 533–40.

Clubb, R. and Mason, G. (2007) 'Natural behavioural biology as a risk factor in carnivore welfare: how analysing species differences could help zoos improve enclosures', *Applied Animal Behaviour Science*, 102: 303–28.

Clubb, R. and Vickery, S. (2006) 'Laboratory stereotypies in carnivores: does pacing stem from hunting, ranging or frustrated escape?', in G. J. Mason (ed.), *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*, Wallingford, Oxon: CABI Publishing, pp. 58–84.

Clubb, R., Rowcliffe, M., Lee, P., Mar, K. U., Moss, C., and Mason, G. (2008) 'Compromised survivorship in zoo elephants', *Science*, 322: 1649.

Clubb, R., Rowcliffe, M., Lee, P., Mar, K. U., Moss, C., and Mason, G. J. (2009) 'Fecundity and population viability in female zoo elephants: problems and possible solutions', *Animal Welfare*, 18: 237–47.

Cocks, L. (2007) 'Factors influencing the well-being and longevity of captive female orang-utans', *International Journal of Primatology*, 28: 429–40.

Coe, J. (1985) 'Design and perception: making the zoo experience real', *Zoo Biology*, 4: 197–208.

Coe, J. (1987) 'What's the message? Exhibit design for education', in *American Association of Zoological Parks and Aquariums Regional Conference Proceedings*, Wheeling, WV: AAZPA, pp. 19–23.

Coe, J. (1989) 'Naturalizing habitats for captive primates', *Zoo Biology*, 8: 117–25.

Coe, J. (1994) 'Landscape immersion: origins and concepts', in J. C. Coe (mod.), *Landscape Immersion Exhibits: How are They Proving as Education Settings? American Zoo and Aquarium Association Convention Proceedings*, Bethesda, MD: AZA, pp. 1–7, available online at **http://www.joncoedesign.com/pub/technical.htm**.

Coe, J. (1996) 'What's the message? Education through exhibit design', in D. Kleiman, M. Allen, K. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago Press, pp. 167–74.

Coe, J. (1997) 'Entertaining zoo visitors and zoo animals: an integrated approach', in *Proceedings of the American Zoo and Aquarium Association Annual Conference*, Bethesda, MD: AZA, pp. 156–62.

Coe, J. (1999) 'An integrated approach to design: how zoo staff can get the best results from new facilities', *First Annual Rhino Keeper Workshop*, 7–8 May, Disney's Wild Animal Kingdom, Orlando, FL.

Coe, J. (2006) 'Naturalistic enrichment', in *Australasian Regional Association of Zoological Parks and Aquaria Conference Proceedings*, Perth Zoo, ARAZPA, pp. 1–9, available online at **http://www.joncoedesign.com/pub/technical.htm**.

Colahan, H. and Breder, C. (2003) 'Primate training at Disney's Animal Kingdom', *Journal of Applied Animal Welfare Science*, 6: 235–46.

Cole, C. and Townsend, C. (1977) 'Parthenogenetic reptiles: new subjects for laboratory research', *Experientia*, 33: 285–9.

Coleman, K. (2011). 'Caring for nonhuman primates in biomedical research facilities: scientific, moral and emotional considerations', *American Journal of Primatology*, 73: 220–5.

Coleman, K. and Maier, A. (2010). 'The use of positive reinforcement training to reduce stereotypic behaviour in rhesus macaques', *Applied Animal Behaviour Science* 124: 142–8.

Colman, R. J., McKiernan, S. H., Aiken, J. M., and Weindruch, R. (2005) 'Muscle mass loss in rhesus monkeys: age of onset', *Experimental Gerontology*, 40: 573–81.

Conde, D. A., Flesness, N., Colchero, F., Jones, O. R., and Scheuerlein, A. (2011). 'An emerging role of zoos to conserve biodiversity', *Science NY*, 331: 1390–1 (plus supporting material).

Conte, E. S. (2004) 'Stress and the welfare of cultured fish', *Applied Animal Behaviour Science*, 86: 205–23.

Conway, W. (1986a) 'The consumption of wildlife by man', *Animal Kingdom*, 7: 18–23.

Conway, W. (1986b) 'The practical difficulties and financial implications of endangered species breeding programmes', *International Zoo Yearbook*, 24/25: 210–19.

Conway, W. (2003) 'The role of zoos in the 21st century', *International Zoo Yearbook*, 38: 7–13.

Conway, W. (2007) 'Entering the 21st century', in A. Zimmerman, M. Hatchwell, L. Dickie, and C. West (eds), *Zoos in the 21st Century: Catalysts for Conservation?*, Cambridge: Cambridge University Press, pp. 12–21.

Conway, W. G. (2011). 'Buying time for wild animals with zoos', *Zoo Biology*, 30: 1–8.

Cook, R. A. and Karesh, W. B. (2012) 'Emerging diseases at the interface of people, domestic animals, and wildlife', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 136–46.

Cook, S. and Hosey, G. R. (1995) 'Interaction sequences between chimpanzees and human visitors at the zoo', *Zoo Biology*, 14: 431–40.

Cooper, J. E. and Cooper, M. E. (2007) 'Importance and application of animal law', in J. E. Cooper and M. E. Cooper (eds), *Introduction to Veterinary and Comparative Forensic Medicine*, Oxford: Blackwell, pp. 42–60.

Cooper, K. A., Harder, J. D., Clawson, D. H., *et al.* (1990) 'Serum testosterone and musth in captive male African and Asian elephants', *Zoo Biology* 9: 297–306.

Cooper, M. E. (2003) 'Zoo legislation', *International Zoo Yearbook*, 38: 81–93.

Cooper, M. E. and Rosser, A. M. (2002) 'International regulation of wildlife trade: relevant legislation and organisations', *Revue Scientifique et Technique de l'Office International des Epizooties*, 21: 103–23.

Cooper, M. R. and Johnson, A. W. (1998) *Poisonous Plants and Fungi in Britain—Animal and Human Poisoning*, London: HMSO.

Cooper, V. J. and Hosey, G. R. (2003) 'Sexual dichromatism and female preference in *Eulemur fulvus* subspecies', *International Journal of Primatology*, 24: 1177–88.

Coote, T. and Loeve, E. (2003) 'From 61 species to five: endemic tree snails of the Society Islands fall prey to an ill-judged biological control programme', *Oryx*, 37: 91–6.

Coote, T., Clarke, D., Hickman, C. S., Murray, J., and Pearce-Kelly, P. (2004) 'Experimental release of endemic *Partula* species, extinct in the wild, into a protected area of natural habitat on Moorea', *Pacific Science*, 58: 429–34.

Cork, S. C. (2000) 'Iron storage disease in birds', *Avian Pathology*, 29: 7–12.

Cornetto, T. and Estevez, I. (2001) 'Behavior of the domestic fowl in the presence of vertical panels', *Poultry Science*, 80: 1455–62.

Corson-White, E. P. (1932) *Diet in Relation to Degenerative Bone Lesions and Fertility*, Report of the Laboratory and Museum of Comparative Pathology, Zoological Society of Philadelphia, pp. 26–8.

Cottle, L., Tamir, D., Hyseni, M., Bühler, D., and Lindemann-Matthies, P. (2010). 'Feeding live prey to zoo animals: response of zoo visitors in Switzerland', *Zoo Biology*, 29: 344–50.

Coulton, L. E., Waran, N. K., and Young, R. J. (1997) 'Effects of foraging enrichment on the behaviour of parrots', *Animal Welfare*, 6: 357–63.

Cousins, D. (2006) 'Review of the use of herb gardens and medicinal plants in primate exhibits in zoos', *International Zoo Yearbook*, 40: 341–50.

Coviello-McLaughlin, G. M., and Starr, S. J. (1997) 'Rodent enrichment devices: evaluation of preference and efficacy', *Contemporary Topics in Laboratory Animal Science*, 36: 66–8.

Cowie, A. (1948) *Pregnancy Diagnosis: A Review*, Reading: Commonwealth Agricultural Bureaus.

Crandall, K. A., Bininda-Emonds, O. R. P., Mace, G. M., and Wayne, R. K. (2000) 'Considering evolutionary processes in conservation biology', *Trends in Ecology and Evolution*, 15: 290–5.

Cranfield, M. R., Graczyk, T. K., and McCutchan, T. F. (2000) 'ELISA antibody test, PCR and a DNA vaccine for use with avian malaria in African penguins', in *Proceedings of the Annual Meeting of the American Association of Zoo Veterinarians*, Yulee, FL: AAZV, p. 39.

Crawshaw, G. (2003) 'Anurans (*Anura*, *Salienta*): frogs, toads', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier.

Cray, C. (2012) 'Diagnosis of aspergillosis in avian species', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 336–42.

Creel, S., Creel, N. M., Mills, M. G. L., and Monfort, S. L. (1997) 'Rank and reproduction in cooperatively breeding African wild dogs: behavioral and endocrine correlates', *Behavioural Ecology*, 8: 298–306.

Cresswell, W., Lind, J., Quinn, L., Minderman, J., and Whitfield, D. P. (2007) 'Ringing or colour-banding does not increase predation mortality in redshanks *Tringa totanus*', *Journal of Avian Biology*, 38: 309–16.

Crissey, S. (2005) 'The complexity of formulating diets for zoo animals: a matrix', *International Zoo Yearbook*, 39: 36–43.

Critser, J. K., Riley, L. K., and Prather, R. S. (2003) 'Application of nuclear transfer technology to wildlife species', in W. Holt, A. Pickard, J. Rodger, and D. Wildt (eds), *Reproductive Science and Integrated Conservation*, Cambridge: Cambridge University Press, pp. 195–208.

Crockett, C. and Bowden, D. (1994) 'Challenging conventional wisdom for housing monkeys', *Laboratory Animals*, 24: 29–33.

Crockett, C., Bowers, C., Sackett, G., and Bowden, D. (1993a) 'Urinary cortisol responses of longtailed macaques to five cage sizes, tethering, sedation and room change', *American Journal of Primatology*, 30: 55–73.

Crockett, C., Bowers, C., Shimoji, M., Leu, M., Bellanca, R., and Bowden, D. (1993b) 'Appetite and urinary cortisol responses to different cage sizes in female pigtailed macaques', *American Journal of Primatology*, 31: 305 (abstract).

Crockett, C. M., Bowers, C. L., Bowden, D. M., and Sackett, G. P. (1994) 'Sex differences in compatibility of pair-housed adult longtailed macaques', *American Journal of Primatology*, 32: 73–94.

Cronin, M. A. (1993) 'Mitochondrial DNA in wildlife taxonomy and conservation biology: cautionary notes', *Wildlife Society Bulletin*, 21: 339–48.

Csuti, B., Sargent, E. L., and Bechert, U. S. (eds) (2001) *The Elephant's Foot: Prevention and Care of Foot Conditions in Captive Asian and African Elephants*, Ames, IA: Iowa State University Press.

Cueto, G. R., Allekotte, R., and Kravetz, F. O. (2000) 'Scurvy in capybaras bred in captivity in Argentina', *Journal of Wildlife Diseases*, 36: 97–101.

Culik, B., Wilson, R., and Bannasch, R. (1993) 'Flipper-bands on penguins: what is the cost of a life-long commitment?', *Marine Ecology Progress Series*, 98: 209–14.

Cunningham, A. A., Frank, M. J., Croft, P., Clarke, D., and Pearce-Kelly, P. (1997) 'Mortality of captive British wartbiter crickets: implications for reintroduction programs', *Journal of Wildlife Diseases*, 33: 673–6.

Cushing, N. and Markwell, K. (2011) 'I can't look: disgust as a factor in the zoo experience', in W. Frost (ed.) *Zoos and Tourism: Conservation, Education, Entertainment?* Bristol: Channel View Publications, pp. 167–78.

D

Dalgetty, G. (2007) 'Zoo bill receives all-party support', *Toronto Observer*, 15 March, available online at http://www.tobserver.com/CYCLEFEB07/15-03-07-DalgettyZoo.html.

Dalley, S. (1993) 'Ancient Mesopotamian gardens and the identification of the Hanging Gardens of Babylon resolved', *Garden History*, 21: 1–13.

Dalton, R. and Buchanan-Smith, H. M. (2005) 'A mixed-species exhibit for Goeldi's monkeys and pygmy marmosets *Callimico goeldii* and *Callithrix pygmaea* at Edinburgh Zoo', *International Zoo Yearbook*, 39: 176–84.

da Nogueira, S. S., Silva, M. G., dos Dias, C. T., Pompéia, S., Cetra, M., and Nogueira-Filho, S. L. G. (2010). 'Social behaviour of collared peccaries (*Pecari tajacu*) under three space allowances', *Animal Welfare*, 19: 243–8.

Dantzer, R. (1994) 'Animal welfare methodology and criteria', *Revue Scientifique et Technique de l'Office International des Epizooties*, 13: 277–302.

D'Août, K., Aerts, P., Clercq, D. D., Schoonaert, K., Vereecke, E., and Elsacker, L. V. (2001) 'Studying bonobo (*Pan paniscus*) locomotion using an integrated setup in a zoo environment: preliminary results', *Primatologie*, 4: 191–206.

da Silva, M. A. M. and da Silva, J. M. C. (2007) 'A note on the relationships between visitor interest and characteristics of the mammal exhibits in Recife Zoo, Brazil', *Applied Animal Behaviour Science*, 105: 223–6.

Davey, G. (2006a) 'Visitor behavior in zoos: a review', *Anthrozoös*, 19: 143–57.

Davey, G. (2006b) 'Relationship between exhibit naturalism, animal visibility and visitor interest in a Chinese zoo', *Applied Animal Behaviour Science*, 96: 93–102.

Davey, G. (2007a). 'An analysis of country, socioeconomic and time factors on worldwide zoo attendance during a 40-year period', *International Zoo Yearbook*, 41: 217–25.

Davey, G. (2007b). 'Public perceptions in urban China toward zoos and their animal welfare', *Human Dimensions of Wildlife*, 12: 367–74.

Davey, G., Henzi, P., and Higgins, L. (2005) 'The influence of environmental enrichment on Chinese visitor behaviour', *Journal of Applied Animal Welfare Science*, 8: 131–40.

Davies, N. B. (1992) *Dunnock Behaviour and Social Evolution*, Oxford: Oxford University Press.

Davis, H. (2002) 'Prediction and preparation: Pavlovian implications of research animals discriminating among humans', *ILAR Journal*, 43: 19–26.

Davis, N., Schaffner, C. M., and Smith, T. E. (2005) 'Evidence that zoo visitors influence HPA activity in spider monkeys (*Ateles geoffroyi rufiventris*)', *Applied Animal Behaviour Science*, 90: 131–41.

Davis, N., Schaffner, C. M. and Wehnelt, S. (2009). 'Patterns of injury in zoo-housed spider monkeys: a problem with males?', *Applied Animal Behaviour Science*, 116: 250–9.

Davis, T. and Ovaska, K. (2001) 'Individual recognition of amphibians: effects of toe clipping and fluorescent tagging on the salamander *Plethodon vehiculum*', *Journal of Herpetology*, 35: 217–25.

Dawkins, M. S. (1983) 'Battery hens name their price: consumer demand theory and the measurement of ethological "needs"', *Animal Behaviour*, 31: 1195–1205.

Dawkins, M. S. (1988) 'Behavioural deprivation: a central problem in animal welfare', *Applied Animal Behaviour Science*, 20: 209–25.

Dawkins, M. S. (1997) 'D. G. M. Wood-Gush Memorial Lecture: Why has there not been more progress in animal welfare research?', *Applied Animal Behaviour Science*, 53: 59–73.

Dawkins, M. S. (2003) 'Behaviour as a tool in the assessment of animal welfare', *Zoology*, 106: 383–7.

Dawkins, M. S. (2006) 'Through animal eyes: what behaviour tells us', *Applied Animal Behaviour Science*, 100: 4–10.

Dawkins, M. S. (2007) *Observing Animal Behaviour*. Oxford: Oxford University Press.

Dawkins, M. S. (2012) *Why Animals Matter: Animal Consciousness, Animal Welfare, and Human Well-being*. Oxford: Oxford University Press.

Dayan, A. (1971) 'Comparative neuropathology of aging: studies of the brain of 47 species of vertebrates', *Brain*, 94: 31–42.

Dayrell, E. and Pullen, K. (2003) 'Post-occupancy evaluation of a red river hog (*Potamochoerus porcus*) enclosure', in T. Gilbert (ed.), *Proceedings of the Fifth Annual Symposium on Zoo Research*, London: Federation of Zoological Gardens of Great Britain and Ireland, pp. 226–30.

Deagle, B. and Tollit, D. (2007) 'Quantitative analysis of prey DNA in pinniped faeces: potential to estimate diet composition?', *Conservation Genetics*, 8: 743–7.

Deardorff, T. L. and Throm, R. (1988) 'Commercial blast-freezing of third-stage *Anisakis simplex* larvae encapsulated in salmon and rockfish', *Journal of Parasitology*, 74: 600–3.

de Azevedo, C. S. and Young, R. J. (2006a) 'Behavioural responses of captive-born greater rheas *Rhea americana* Linnaeus (Rheiformes: Rheidae) submitted to antipredator training', *Revista Brasileira de Zoologia*, 23: 186–93.

de Azevedo, C. S. and Young, R. J. (2006b) 'Do captive-born greater rheas *Rhea americana* Linnaeus (Rheiformes: Rheidae) remember antipredator training?', *Revista Brasileira de Zoologia*, 23: 194–201.

Defra (Department for Environment, Food and Rural Affairs) (2002) *Zoo Inspectors' Training Seminar*, 5–7 April, Bath University, available online at **http://www.defra. gov.uk/wildlife-countryside/gwd/zoo-inspectors/bath-seminar2002.pdf**.

Defra (Department for Environment, Food and Rural Affairs) (2004) *Secretary of State's Standards of Modern Zoo Practice* (revised edn), available online at **http://www. defra.gov.uk/wildlife-countryside/gwd/zooprac/index.htm**.

Defra (Department for Environment, Food and Rural Affairs) (2007a) *Animal Welfare: Protecting Domestic or Captive Animals from Cruelty*, available online at **http://www. defra.gov.uk/animalh/welfare/domestic/index.htm**.

Defra (Department for Environment, Food and Rural Affairs) (2007b) *Zoos Forum Handbook*, available online at **http://www.defra.gov.uk/wildlife-countryside/gwd/ zoosforum/handbook/**.

Defra (Department for Environment, Food and Rural Affairs) (2008) *Animal Welfare Act 2006*, available online at **http://www.defra.gov.uk/animalh/welfare/act/index.htm**.

Defra (Department for Environment, Food and Rural Affairs) (2012a) Secretary of State's Standards of Modern Zoo Practice (SSSMZP), available online at **http://www. defra.gov.uk**.

Defra (2012b) *Zoos Expert Committee Handbook*, available online at **http://www.defra.gov.uk**.

DfES (Department for Education and Skills) (2006) *Learning Outside the Classroom Manifesto*, Nottingham: DfES Publications.

DeGrazia, D. (2002) *Animal Rights: A Very Short Introduction*, Oxford: Oxford University Press.

Delfour, F., and Beyer, H. (2012) 'Assessing the effectiveness of environmental enrichment in bottlenose dolphins (*Tursiops truncatus*)', *Zoo Biology*, 31: 137–50.

Dembiec, D., Snider, R., and Zanella, A. (2004) 'The effects of transport stress on tiger physiology and behaviour', *Zoo Biology*, 23: 335–46.

Dempsey, J. L. (2004) 'Fruit bats: nutrition and dietary husbandry', *AZA Nutrition Advisory Group Handbook*, Fact Sheet 14, available online at **http://www.nagonline.net**.

de Passillé, A. M., Rushen, J., Ladewig, J., and Petherick, C. (1996) 'Dairy calves' discrimination of people based on previous handling', *Journal of Animal Science*, 74: 969–74.

de Rouck, M., Kitchener, A. C., Law, G., and Nelissen, M. (2005) 'A comparative study of the influence of social housing conditions on the behaviour of captive tigers (*Panthera tigris*)', *Animal Welfare*, 14: 229–38.

Desmond, T. and Laule, G. (1994) 'Use of positive reinforcement training in the management of species for reproduction', *Zoo Biology*, 13: 471–7.

de Vos, V. (2003) 'Anthrax', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 696–9.

de Waal, F. B. M. (1982) *Chimpanzee Politics*, London: Jonathan Cape.

de Waal, F. B. M. (1989) 'The myth of a simple relation between space and aggression in captive primates', *Zoo Biology (Supplement)*, 1: 141–8.

Dewsbury, D. A. (1992) 'Studies on rodent–human interactions in animal psychology', in H. Davis and D. Balfour (eds), *The Inevitable Bond: Examining Scientist–Animal Interactions*, Cambridge: Cambridge University Press, pp. 27–43.

Diamond, M. C. (2001) 'Response of the brain to enrichment', *Anais da Academia Brasileira de Ciencias*, 73: 211–20.

Dickie, L. (2009) The sustainable zoo: an introduction, *International Zoo Yearbook*, 43: 1–5.

Dickie, L. A., Bonner, J. P., and West, C. (2007) '*In situ* and *ex situ* conservation: blurring the boundaries between zoos and the wild', in A. Zimmerman, M. Hatchwell, L. A. Dickie, and C. West (eds), *Zoos in the 21st Century*, Cambridge: Cambridge University Press, pp. 220–35.

Dickinson, H. C. and Fa, J. E. (1997) 'Ultraviolet light and heat source selection in captive spiny-tailed iguanas (*Oplurus cuvieri*)', *Zoo Biology*, 16: 391–401.

Dierenfeld, E. S. (1997a) 'Captive wild animal nutrition: a historical perspective', *Proceedings of the Nutrition Society*, 56: 989–99.

Dierenfeld, E. S. (1997b) 'Orang-utan nutrition', in C. Sodaro (ed.), *Orang-utan SSP Husbandry Manual*, Brookfield, IL: Orang-utan SSP and Brookfield Zoo.

Dierenfeld, E. S. (2005) 'Advancing zoo animal nutrition through global synergy', *International Zoo Yearbook*, 39: 29–35.

Dierenfeld, E. S., Atkinson, S., Craig, A. M., Walker, K. C., Streich, W. J., and Clauss, M. (2005) 'Mineral concentrations in serum/plasma and liver tissue of captive and free-ranging Rhinoceros species', *Zoo Biology*, 24: 51–72.

Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., and van Noordwijk, A. J. (2002) 'Repeatability and heritability of exploratory behaviour in great tits from the wild', *Animal Behaviour*, 64: 929–38.

Dingemanse, N. J., Kazem, A .J. N., Reale, D., and Wright, J. (2010) 'Behavioural reaction norms: animal personality meets individual plasticity', *Trends in Ecology and Evolution*, 25: 81–9.

Disney, W., Green, J., Forsythe, K., Wiemers, J., and Weber, S. (2001) 'Benefit–cost analysis of animal identification for disease prevention and control', *Revue Scientifique et Technique de l'Office International des Epizooties*, 20: 385–405.

Dobbs, T. and Fry, A. (2008) 'The development and progression of the primate enrichment timetables at Paignton Zoo', in V. Hare (ed.), *Proceedings of the Eighth Conference on Environmental Enrichment*, San Diego, CA: The Shape of Enrichment.

Doerfler, R. L. and Peters, K. J. (2006) 'The relativity of ethical issues in animal agriculture related to different cultures and production conditions', *Livestock Science*, 103: 257–62.

Dol, M., Fentener van Vlissingen, M., Kasanmoentalib, S., Visser, T., and Zwart, H. (1999) (eds) *Recognizing the Intrinsic Value of Animals Beyond Animal Welfare*, Assen, The Netherlands: van Gorcum.

Dolins, F. L. (1999) *Attitudes to Animals: Views in Animal Welfare*, Cambridge: Cambridge University Press.

Dollinger, P. (2007) ' "Balai" Directive of the European Union: difficult veterinary legislation', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (6th edn), St Louis, MO: Saunders Elsevier, pp. 68–74.

Donahue, J. and Trump, E. (2006) *The Politics of Zoos: Exotic Animals and their Protectors*, DeKalb, IL: Northern Illinois University Press.

Doncaster, C. P., Dickman, C. R., and Macdonald, D. W. (1990) 'Feeding ecology of red foxes (*Vulpes vulpes*) in the City of Oxford, England', *Journal of Mammalogy*, 71: 188–94.

Donoghue, A. M., Blanco, J. M., Gee, G. F., Kirby, Y. K., and Wildt, D. E. (2003) 'Reproductive technologies and challenges in avian conservation and management', in W. Holt, A. Pickard, J. Rodger, and D. Wildt (eds), *Reproductive Science and Integrated Conservation*, Cambridge: Cambridge University Press, pp. 321–37.

Donohue, K. C. and Dufty, A. M. (2006) 'Sex determination of red-tailed hawks (*Buteo jamaicensis calurus*) using DNA analysis and morphometrics', *Journal of Field Ornithology*, 77: 74–9.

Dooley, M. and Pineda, M. (2003) 'Patterns of reproduction', in M. H. Pineda and M. P. Dooley (eds), *McDonald's Veterinary Endocrinology and Reproduction*, Oxford: Blackwell, pp. 377–94.

Dorey, N. R., Rosales-Ruiz, J., Smith, R., and Lovelace, B. (2009) Functional analysis and treatment of self-injury in a captive olive baboon, *Journal of Applied Behavior Analysis*, 42: 785–94.

Dorman, N. and Bourne, D. C. (2010). Canids and ursids in mixed-species exhibits. *International Zoo Yearbook* 44: 75–86.

Douglas-Hamilton, I., Bhalla, S., Wittemyer, G., and Vollrath, F. (2006) 'Behavioural reactions of elephants towards a dying and deceased matriarch', *Applied Animal Behaviour Science*, 100: 87–102.

Duckler, G. (1998) 'An unusal osteological formation in the posterior skulls of captive tigers (*Panthera tigris*)', *Zoo Biology*, 17: 135–42.

Dudink, S., Simonse, H., Marks, I., Jonge, F. H., and Spruijt, B. M. (2006) 'Announcing the arrival of enrichment increases play behaviour and reduces weaning-stress-induced behaviours of piglets directly after weaning', *Applied Animal Behaviour Science*, 101: 86–101.

Duncan, I. J. H. (1978) 'The interpretation of preference tests in animal behaviour', *Applied Animal Ethology*, 4: 197–200.

Duncan, I. J. H. (1993) 'Welfare is to do with what animals feel', *Journal of Agricultural and Environmental Ethics*, 6: 8–14.

Duncan, I. J. H. (2005) 'Science-based assessment of animal welfare: farm animals', *Revue Scientifique et Technique de l'Office International des Epizooties*, 24: 483–92.

Duncan, I. J. H. (2006) 'The changing concept of animal sentience', *Applied Animal Behaviour Science Sentience in Animals*, 100: 11–19.

Duncan, I. J. H. and Fraser, D. (1997) 'Understanding animal welfare', in M. Appleby and B. Hughes (eds), *Animal Welfare*, Wallingford, Oxon: CABI Publishing, pp. 19–31.

Duncan, I. J. H. and Olsson, I. A. S. (2001) 'Environmental enrichment: from flawed concept to pseudo-science', *Proceedings of the 35th International Congress of the International Society for Applied Ethology*, Davis, CA: Center for Animal Welfare, University of California at Davis, p. 73.

Duncan, L. M. and Pillay, N. (2012) 'Volunteer experience influences the conclusions of behavioural experiments', *Applied Animal Behaviour Science*, 140: 179–87.

Duncan, M. (2003) 'Fungal diseases in all taxa', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 727–32.

Durnin, M., Palsbell, P. J., Ryder, O., and McCullough, D. (2007) 'A reliable genetic technique for sex determination of giant panda (*Ailuropoda melanoleuca*) from non-invasively collected hair samples', *Conservation Genetics*, 8: 715–20.

Durrell, G. (1976) *The Stationary Ark*, London: Collins.

E

EAP (Exhibited Animal Protection Act) (2008) '*Standards for Exhibiting Seals in New South Wales*' (supporting regulations to the *Exhibited Animals Protection Act* (NSW)1986).

Earnhardt, J. M. (2010) 'The role of captive populations in reintroduction programs', in D. G. Kleiman, K. V. Thompson, and C. Kirk Baer (eds) *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: University of Chicago Press, pp. 268–80.

Eaton, G. G., Kelley, S. T., Axthelm, M. K., Iliff-Sizemore, S. A., and Shiigi, S. M. (1994) 'Psychological well-being in paired adult female rhesus (*Macaca mulatta*)', *American Journal of Primatology*, 33: 89–99.

EAZA (European Association of Zoos and Aquaria) (2003) 'From the EAZA Office: fifteen years E(C)AZA', *EAZA Newsletter*, 44: 5–8.

EAZA (European Association of Zoos and Aquaria) (2008) *EAZA Education Standards*, Amsterdam: EAZA Executive Office.

EC (European Commission) (1999) 'Council Directive 1999/22/EC of 29 March (1999) relating to the keeping of wild animals in zoos', *Official Journal of the European Communities*, L94/24 (09/04/1999).

EC (European Commission) (2006) *The Convention on Biological Diversity: Implementation in the European Union*, Luxembourg: Office for Official Publications of the European Communities.

Edberg, S. (2004) 'The algae: marine mammal enrichment at Kolmarden Zoo', *The Shape of Enrichment*, 13: 1–3.

EFSA (European Food Safety Authority) (2008) 'Avian influenza', available online at http://www.efsa.europa.eu/EFSA/KeyTopics/efsa_locale-1178620753812_AvianInfluenza.htm.

Egliston, K., McMahon, C., and Austin, M. (2007) 'Stress in pregnancy and infant HPA axis function: conceptual and methodological issues relating to the use of salivary cortisol as an outcome measure', *Psychoneuroendocrinology*, 32: 1–32.

Eisenberg, J. and Kleiman, D. (1977) 'The usefulness of behaviour studies in developing captive breeding programmes for mammals', *International Zoo Yearbook*, 17: 81–8.

Ellis, D. and Dein, F. (1996) 'Special techniques: part E flight restraint', in D. Ellis, G. Gee, and C. Mirande, *Cranes: Their Biology, Husbandry and Conservation*, Washington, DC/Baraboo, WI: US Department of the Interior, National Biological Service/International Crane Foundation, pp. 241–4.

Elson, H. (2007) 'An investigation into the short-term effects of environmental enrichment on the behaviour of psittacines in captivity', unpublished PhD thesis, Trinity College, University of Dublin.

Elson, H. and Marples, N. (2001) 'Effects of environmental enrichment on parrots in captivity', in S. Wehnelt and C. Hudson (eds), *Proceedings of the Third Annual Symposium on Zoo Research*, London: BIAZA, pp. 1–8.

Elwood, R. W. (2011) 'Pain and suffering in invertebrates', *ILAR Journal*, 52: 175–84.

Elwood, R. W., Barr, S., Patterson, L. (2009) 'Pain and stress in crustaceans?' *Applied Animal Behaviour Science,* 118: 128–36.

Embury, A. S. (1992) 'Gorilla rainforest at Melbourne Zoo', *International Zoo Yearbook*, 31: 203–13.

Erickson, G. M., Lappin, A. K., and Vliet, K. A. (2003) 'Comparison of the bite-force performance between long-term captive and wild American alligators (*Alligator mississippiensis*)', *Journal of Zoology*, 262: 21–8.

Erlacher-Ried, C., Dunn, J. L., Champ, T., Macha, L., Mazzaro, L., and Tuttle, A. D. (2012) 'Evaluation of potential variables contributing to the development and duration of plantar lesions in a population of aquarium-maintained African penguins (*Spheniscus demersus*)', *Zoo Biology*, 31: 291–305.

Erwin, J. (1979) 'Aggression in captive macaques: interactions of social and spatial factors', in J. Erwin, T. Maple, and G. Mitchell (eds), *Captivity and Behaviour of Primates in Breeding Colonies, Laboratories and Zoos*, New York: Van Nostrand–Reinhold, pp. 139–71.

Erwin, J. and Deni, R. (1979) 'Strangers in a strange land: abnormal behaviours or abnormal environments?', in J. Erwin, T. L. Maple and G. Mitchell (eds), *Captivity and Behaviour of Primates in Breeding Colonies, Laboratories and Zoos*, New York, NY: Van Nostrand–Reinhold, pp. 1–28.

Essler, W. and Folkjun, G. (1961) 'Determination of physiological rhythms of unrestrained animals by radio telemetry', *Nature*, 190: 90–1.

Estep, D. Q. and Baker, S. C. (1991) 'The effects of temporary cover on the behavior of socially housed stumptailed macaques (*Macaca arctoides*)', *Zoo Biology*, 10: 465–72.

Estep, D. Q. and Hetts, S. (1992) 'Interactions, relationships, and bonds: the conceptual basis for scientist–animal relations', in H. Davis and D. Balfour (eds), *The Inevitable Bond: Examining Scientist–Animal Interactions*, Cambridge: Cambridge University Press, pp. 6–26.

Eurogroup for Animal Welfare (2006) *Report on the Implementation of the EU Zoo Directive*, available online at http://www.eurogroupanimalwelfare.org/policy/pdf/zooreportmar2006.pdf.

Evans, J. E., Cuthill, I. C., and Bennett, A. T. D. (2006) 'The effect of flicker from fluorescent lights on mate choice in captive birds', *Animal Behaviour*, 72: 393–400.

Ewbank, R. (1985) 'Behavioral responses to stress in farm animals', in G. Moberg (ed.), *Animal Stress*, Baltimore, MD: Waverly Press, pp. 71–9.

Ewer, R. F. (1968) *Ethology of Mammals*, London: Elek Books.

Exner, C. and Unshelm, J. (1997) 'Climatic condition and airborne contaminants in buildings of wild cats kept in zoos', *Zentralblatt für Hygiene und Umweltmedizin*, 199: 497–512.

F

Fa, J. E. (1989) 'Influence of people on the behaviour of display primates', in E. F. Segal (ed.), *Housing, Care and Psychological Well-Being of Captive and Laboratory Primates*, Park Ridge, IL: Noyes Publications, pp. 270–90.

Fa, J. E., Funk, S. M., and O'Connell, D. (2011) *Zoo Conservation Biology*, Cambridge: Cambridge University Press.

Fàbregas, M. and Guillén-Salazar, F. (2007) 'Social compatibility in a newly formed all-male group of white crowned mangabeys (*Cercocebus atys lunulatus*)', *Zoo Biology*, 26: 63–9.

Fàbregas, M. C., Guillén-Salazar, F., and Garces-Narro, C. (2012) 'Do naturalistic enclosures provide suitable environments for zoo animals?', *Zoo Biology*, 31: 362–73.

Fairbanks, L. A., Newman, T. K., Bailey, J. N., *et al.* (2004) 'Genetic contributions to social impulsivity and aggressiveness in vervet monkeys', *Biological Psychiatry*, 55: 642–7.

Falk, J. H., Reinhard, E. M., Vernon, C. L., Bronnenkant, K., Heimlich, J. E., and Deans, N. L. (2007) *Why Zoos and Aquariums Matter: Assessing the Impact of a Visit to a Zoo or Aquarium*, Silver Springs, MD: AZA.

Falk, J. H., Heimlich, J. E., Vernon, C. L., and Bronnenkant, K. (2010). Critique of a critique: do zoos and aquariums promote attitude change in visitors? *Society and Animals*, 18: 415–19.

Farmer, H. and Melfi, V. (2008) 'Is it music to their ears?', in V. Hare (ed.), *Proceedings of the Eighth Conference on Environmental Enrichment*, San Diego, CA: The Shape of Enrichment.

Farmer, H. L., Plowman, A. B., and Leaver, L. A. (2011). 'Role of vocalisations and social housing in breeding in captive howler monkeys (*Alouatta caraya*)', *Applied Animal Behaviour Science* 134: 177–83.

Farrell, M. A., Barry, E., and Marples, N. (2000) 'Breeding behavior in a flock of Chilean flamingos (*Phoenicopterus chilensis*) at Dublin Zoo', *Zoo Biology*, 19: 227–37.

Faust, L. J. and Thompson, S. D. (2000). Birth sex ratio in captive mammals: patterns, biases, and the implications for management and conservation. *Zoo Biology*, 19: 11–25.

Faust L. J., Earnhardt, J. E., and Thompson, S. D. (2006) 'Is reversing the decline of Asian elephants in captivity possible? An individual-based modeling approach', *Zoo Biology*, 25: 201–18.

FAWC (Farm Animal Welfare Council) (1992) 'FAWC updates the five freedoms', *Veterinary Record*, 131: 357.

Fekete, J. M., Norcross, J. L., and Newman, J. D. (2000) 'Artificial turf foraging boards as environmental enrichment for pair-housed female squirrel monkeys', *Contemporary Topics in Laboratory Animal Science*, 39: 22–6.

Fenolio, D. B., Graening, G. O., Collier, B. A., and Stout, J. F. (2006) 'Coprophagy in a cave-adapted salamander: the importance of bat guano examined through nutritional and stable isotope analyses', *Proceedings of the Royal Society Series B: Biological Sciences*, 273: 439–43.

Fernandez, E. J. and Timberlake, W. (2008) Mutual benefits of research collaborations between zoos and academic institutions. *Zoo Biology*, 27: 470-487.

Fernandez, E. J., Tamborski, M. A., Pickens, S. R., and Timberlake, W. (2009) 'Animal–visitor interactions in the modern zoo: conflicts and interventions', *Applied Animal Behaviour Science*, 120: 1–8.

Fernandez, L. T., Bashaw, M. J., Sartor, R. L., Bouwens, N. R., and Maki, T. S. (2008) 'Tongue twisters: feeding enrichment to reduce oral stereotypy in giraffe', *Zoo Biology* 27: 200–12.

Ferner, J. (1979) 'A review of marking techniques for amphibians and reptiles', in Society for the Study of Amphibians and Reptiles, *Herpetological Circular No. 9*, Shoreview, MN: SSAR.

Festa-Bianchet, M. and Apollonio, M. (2003) *Animal Behaviour and Wildlife Conservation*, Washington, DC: Island Press.

Fidgett, A. (2005) 'Standardizing nutrition information within husbandry guidelines: the essential ingredients', *International Zoo Yearbook*, 39: 132–8.

Fidgett, A. and Dierenfeld, E. S. (2007) 'Minerals and stork nutrition', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (6th edn), St Louis, MO: Saunders Elsevier, pp. 206–13.

Fidgett, A. and Plowman, A. (2009). *Zoo Research Guidelines on Nutrition and Diet Evaluation.* London: BIAZA.

Fidgett, A., Clauss, M., Ganslosser, U., Hatt, J. M., and Niijboer, J. (eds) (2003) *Zoo Animal Nutrition*, Vol. II, Fürth, Germany: Filander Verlag.

Fidgett, A., Clauss, M., Eulenberger, K., *et al.* (eds) (2006) *Zoo Animal Nutrition*, Vol. III, Fürth, Germany: Filander Verlag.

Fiedeldey, A. (1994) 'Wild animals in a wilderness setting: an ecosystemic experience?', *Anthrozoös*, 7: 113–23.

Filadelfi, A. and Castrucci, A. (1996) 'Comparative aspects of the pineal/melatonin system in poikilothermic vertebrates', *Journal of Pineal Research*, 20: 175–86.

Finlay, T. W. and Maple, T. L. (1986) 'A survey of research in American zoos and aquariums', *Zoo Biology*, 5: 261–8.

Finlay, T. W., James, L. R., and Maple, T. L. (1988) 'People's perceptions of animals: the influence of zoo environment', *Environment and Behavior*, 20: 506–28.

Fish, K. D., Sauther, M. L., Loudon, J. E., and Couzzo, F. P. (2007) 'Coprophagy by wild ring-tailed lemurs (*Lemur catta*) in human-disturbed locations adjacent to the Beza Mahafaly Special Reserve, Madagascar', *American Journal of Primatology*, 69: 713–18.

Fisher, J. and Hinde, R. A. (1949) 'The opening of milk bottles by birds', *British Birds*, 42: 347–57.

Fisher, R. A. (1930) *The Genetical Theory of Natural Selection*, Oxford: Clarendon Press.

Fitch, H. and Fagan, D. A. (1982) 'Focal palatine erosion associated with dental malocclusion in captive cheetahs', *Zoo Biology*, 1: 295–310.

Flach, E. (2003) '*Cervidae* and *Tragulidae*', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 634–49.

Flach, E., Stevenson, M. F., and Henderson, G. M. (1990) 'Aspergillosis in gentoo penguins (*Pygoscelis papua*) at Edinburgh Zoo, 1964–1988', *Veterinary Record*, 126: 81–5.

Flammer, K. (2003) 'Chlamydiosis', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 718–23.

Flecknell, P. and Molony, V. (2003) 'Pain and injury', in M. C. Appleby and B. O. Hughes (eds), *Animal Welfare*, Wallingford, Oxon: CABI Publishing, pp. 63–73.

Flecknell, P. and Waterman-Pearson, A. (2000) *Pain Management in Animals*, London: W. B. Saunders.

Fleetwood, A. J. and Furley, C. W. (1990) 'Spongiform encephalopathy in an eland', *Veterinary Record*, 126: 408–9.

Flesness, N. R. (2003) 'International Species Information System (ISIS): over 25 years of compiling global animal data to facilitate collection and population management', *International Zoo Yearbook*, 38: 53–61.

Flesness, N. R., Lukens, D. R., Jr, Porter, S. B., Wilson, C. R., and Grahn, L. V. (1995). 'ISIS and studbooks, very high census correlation for the North American zoo population: a reply to Earnhardt, Thompson, and Willis', *Zoo Biology*, 14: 509–17.

Fletcher, W. J., Fielder, D. R., and Brown, I. W. (1989) 'Comparison of freeze- and heat-branding techniques to mark the coconut crab *Birgus latro* (Crustacea, Anomura)', *Journal of Experimental Marine Biology and Ecology*, 127: 245–51.

Flew, A. (ed.) (1979) *A Dictionary of Philosophy*, London: Pan.

Fooks, A. R., Brookes, S. M., Johnson, N., McElhinney, L. M., and Hutson, A. M. (2003) 'European bat lyssaviruses: an emerging zoonosis', *Epidemiology and Infection*, 131: 1029–39.

Foose, T. J. (1980) 'Demographic management of endangered species in captivity', *International Zoo Yearbook*, 20: 154–66.

Forthman, D. L., Elder, S. D., Bakeman, R., Kurkowski, T. W., Noble, C. C., and Winslow, S. W. (1992) 'Effects of feeding enrichment on behavior of three species of captive bears', *Zoo Biology*, 11: 187–95.

Forthman-Quick, D. L. (1984) 'An integrative approach to environmental engineering in zoos', *Zoo Biology*, 312: 65–77.

Fowler, M. E. (2007) 'Foot disorders', in M. E. Fowler and S. K. Mikota (eds), *Biology, Medicine and Surgery of Elephants*, Basingstoke: Wiley–Blackwell, pp. 271–90.

Fowler, M. E. and Miller, R. E. (eds) (1993) *Zoo and Wild Animal Medicine* (3rd edn), Philadelphia, PA: W. B. Saunders.

Fowler, M. E. and Miller, R. E. (eds) (1999) *Zoo and Wild Animal Medicine* (4th edn), Philadelphia, PA: W.B. Saunders.

Fowler, M. E. and Miller, R. E. (eds) (2003) *Zoo and Wild Animal Medicine* (5th edn), St Louis, MO: Saunders Elsevier.

Fowler, M. E. and Miller, R. E. (eds) (2008) *Zoo and Wild Animal Medicine: Current Therapy* (6th edn), St Louis, MO: Saunders Elsevier.

Fowler, M. E. and Miller, R. E. (eds) (2012) *Zoo and Wild Animal Medicine: Current Therapy*, Vol. 7, St Louis, MO: Saunders Elsevier.

Francis, C. D., Kleist, N. J., Ortega, C. P., and Cruz, A. (2012) 'Noise pollution alters ecological services: enhanced pollination and disrupted seed dispersal', *Proceedings of the Royal Society of London Series B: Biological Sciences*, 279: 2727–35.

Frankham, R. (2002) 'Relationship of genetic variation to population size in wildlife', *Conservation Biology*, 10: 1500–8.

Frankham, R. (2008) 'Genetic adaptation to captivity in species conservation programs', *Molecular Ecology*, 17: 325–33.

Frankham, R. (2010) 'Challenges and opportunities of genetic approaches to biological conservation', *Biological Conservation*, 143: 1919–27.

Frankham, R., Hemmer, H., Ryder, O., *et al.* (1986) 'Selection of captive populations', *Zoo Biology*, 5: 127–38.

Frankham, R., Ballou, J. D., and Briscoe, D. A. (2002) *Introduction to Conservation Genetics*, Cambridge: Cambridge University Press.

Frankham, R., Ballou, J. D., and Briscoe, D. A. (2004) *A Primer of Conservation Genetics*, Cambridge: Cambridge University Press.

Fraser, A. F. and Broom, D. M. (1990) *Farm Animal Behaviour and Animal Welfare* (3rd edn), London: Baillière Tindall.

Fraser, D. (2008) *Understanding Animal Welfare*, Oxford: Blackwell.

Fraser, D. and Matthews, L. R. (1997) 'Preference and motivation testing', in M. Appleby and B. Hughes (eds), *Animal Welfare*, Wallingford, Oxon: CABI Publishing, pp. 159–72.

Fraser, D. J. and Bernatchez, L. (2001) 'Adaptive evolutionary conservation: towards a unified concept for defining conservation units', *Molecular Ecology*, 10: 2741–52.

Fraser, D. J., Ritchie, J., and Fraser, A. (1975) 'The term "stress" in a veterinary context', *British Veterinary Journal*, 131: 653–62.

Fraser, J. and Sickler, J. (2009). Measuring the cultural impact of zoos and aquariums. *International Zoo Yearbook*, 43: 103–12.

Frediani, K. L. (2009) 'The ethics of plant use in zoos: informing selection choices, uses and management strategies', *International Zoo Yearbook* 43:1, 29–52.

Freeland, W. J. (1991) 'Plant secondary metabolites: biochemical coevolution with herbivores', in R. T. Palo and C. T. Robbins (eds), *Plant Chemical Defenses Against Mammalian Herbivory*, Boca Raton, FL: CRC Press, pp. 61–82.

Freeman, H. D. and Gosling, S. D. (2010). Personality in nonhuman primates: a review and evaluation of past research. *American Journal of Primatology*, 72: 653–671.

Freeman, E., Wiess, E., and Brown, J. (2004) 'Examination of the interrelationships of behavior, dominance status, and ovarian activity in captive Asian and African elephants', *Zoo Biology*, 23: 431–48.

Frézard, A. and Le Pape, G. (2003) 'Contribution to the welfare of captive wolves (*Canis lupus lupus*): a behavioral comparison of six wolf packs', *Zoo Biology*, 22: 33–44.

Friend, T. H. and Parker, M. L. (1999) 'The effect of penning versus picketing on stereotypic behavior of circus elephants', *Applied Animal Behaviour Science*, 64: 213–25.

Frost, W. (ed.) (2011) *Zoos and Tourism: Conservation, Education, Entertainment?* Bristol: Channel View Publications.

Fry, A. and Dobbs, T. (2005) 'From junk to enrichment: uses for a camera film canister', *The Shape of Enrichment*, 14: 1–3.

Frye, F. L. (1992) *Biomedical and Surgical Aspects of Captive Reptile Husbandry*, Melbourne, FL: Krieger.

Frynta, D. D., Lisková, S. S., Bültmann, S. S., and Burda, H. H. (2010) 'Being attractive brings advantages: the case of parrot species in captivity', *PLoS One* 5: e12568.

G

Galis, F., Wagner, G., and Jackson, E. (2003) 'Why is limb regeneration possible in amphibians but not in reptiles, birds and mammals?', *Evolution and Development*, 5: 208–20.

Garcia, L. S. (1999) *Practical Guide to Diagnostic Parasitology*, Washington, DC: ASM Press.

Garner, J. P. and Mason, G. J. (2002) 'Evidence for a relationship between cage stereotypies and behavioural disinhibition in laboratory rodents', *Behavioural Brain Research*, 136: 83–92.

Garner, J. P., Meehan, C. L., and Mench, J. A. (2003) 'Stereotypies in caged parrots, schizophrenia and autism: evidence for a common mechanism', *Behavioural Brain Research*, 145: 125–34.

Garner, J. P., Meehan, C. L., Famula, T. R., and Mench, J. A. (2006) 'Genetic, environmental, and neighbor effects on the severity of stereotypies and feather picking in orange-winged Amazon parrots (*Amazona amazonica*): an epidemiological study', *Applied Animal Behaviour Science*, 96: 153–68.

Garner, R. (2002) 'First "submarium" matches success of Eden Project', *The Independent*, 28 December 2002.

Gartrell, B. D., Raidal, S. R., and Jones, S. M. (2003) 'Renal disease in captive swift parrots (*Lathamus discolor*): clinical findings and disease management', *Journal of Avian Medicine and Surgery*, 17: 213–23.

Gascon, C., Collins, J. P., Moore, R. D., Church, D. R., McKay, J. E., and Mendelson, J. R., III (eds) (2007) *Amphibian Conservation Action Plan*, Gland/Cambridge: IUCN/SSC Amphibian Specialist Group.

Gauthier-Clerc, M. and Le Maho, Y. (2001) 'Beyond bird marking with rings', *Ardea (Special Issue)*, 89: 221–30.

Gehrmann, W., Ferguson, G., Odom, T., Roberts, D., and Barcelone, W. (1991) 'Early growth and bone mineralization of the iguanid lizard *Sceloporus occidentalis* in captivity: is vitamin D supplementation or ultraviolet B irradiation necessary?', *Zoo Biology*, 10: 409–16.

Geissmann, T. (2007) 'Status reassessment of the gibbons: results of the Asian Primate Red List Workshop 2006', *Gibbon Journal*, 3: 5–15.

Genty, E. and Roeder, J.-J. (2006) 'Self-control: why should sea lions, *Zalophus californianus*, perform better than primates?', *Animal Behaviour*, 72: 1241–7.

Geraci, J. R. (1986) 'Nutrition and nutritional disorders', in M. E. Fowler (ed.), *Zoo and Wild Animal Medicine* (2nd edn), Philadelphia, PA: W. B. Saunders, pp. 760–4.

Gerald, M., Weiss, A., and Ayala, J. (2006) 'Artifical colour treatment mediates aggression among unfamiliar vervet monkeys (*Cercopithecus aethiops*): a model for introducing primates with colourful sexual skin', *Animal Welfare*, 15: 363–9.

Gesualdi, J. (2001) 'North America: licensing and accreditation', in C. E. Bell (ed.), *Encyclopedia of the World's Zoos*, Chicago, IL/London: Fitzroy Dearborn, pp. 883–5.

Gilbert, M. and Philippa, J. (2012) 'Avian influenza H5N1 virus: epidemiology in wild birds, zoo outbreaks, and zoo vaccination policy', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Elsevier Saunders, pp. 343–8.

Gillespie, D., Frye, F. L., Stockham, S. L., and Fredeking, T. (2001) 'Blood values in wild and captive Komodo dragons (*Varanus komodoensis*)', *Zoo Biology*, 19: 495–509.

Gittleman, J. L. (1994) 'Are the pandas successful specialists or evolutionary failures?', *BioScience*, 44: 456–64.

Gittleman, J. L. and Thompson, S. D. (1988) 'Energy allocation in mammalian reproduction', *American Zoologist*, 28: 863–75.

Glander, K. E. (1994) 'Non-human primate self-medication with wild plant foods', in N. Etkin (ed.), *Eating on the Wild Side: The Pharmacologic, Ecologic and Social Implications of Using Noncultigens*, Tucson, AZ: University of Arizona Press, pp. 227–39.

Glatston, A. R. (1998) 'The control of zoo populations with special reference to primates', *Animal Welfare*, 7: 269–81.

Glatston, A. R., Geilvoet-Soeteman, E., Hora-Pecek, E., and van Hooff, J. A. R. A. M. (1984) 'The influence of the zoo environment on social behaviour of groups of cotton-topped tamarins, *Saguinus oedipus oedipus*', *Zoo Biology*, 3: 241–53.

Glatt, S. E., Francl, K. E., and Scheels, J. L. (2008) 'A survey of current dental problems and treatments of zoo animals', *International Zoo Yearbook*, 42: 206–13.

Goerke, B., Fleming, L., and Creel, M. (1987) 'Behavioral changes of a juvenile gorilla after a transfer to a more naturalistic environment', *Zoo Biology*, 6: 283–95.

Golani, I., Kafkafi, N., and Drai, D. (1999) 'Phenotyping stereotypic behaviour: collective variables, range of variation and predictability', *Applied Animal Behaviour Science*, 65: 191–220.

Golub, M. S., Keen, C. L., and Hendrickx, A. G. (1990) 'Food preference of young rhesus monkeys fed marginally zinc deficient diets', *Primates*, 32: 49–59.

Gomendio, M., Cassinello, J., and Roldan, E. (2000) 'A comparative study of ejaculate traits in three endangered ungulates with different levels of inbreeding: fluctuating asymmetry as an indicator of reproductive and genetic stress', *Proceedings of the Royal Society of London Series B: Biological Sciences*, 267: 875–82.

Gomez, J-.C. (2005) 'Species comparative studies and cognitive development', *Trends in Cognitive Sciences Developmental Cognitive Neuroscience*, 9: 118–25.

Goossens, E., Dorny, P., Boomker, J., Vercammen, F., and Vercruysse, J. (2005) 'A 12-month survey of the gastro-intestinal helminths of antelopes, gazelles and giraffids kept at two zoos in Belgium', *Veterinary Parasitology*, 127: 303–12.

Gore, M., Hutchins, M., and Ray, J. (2006) 'A review of injuries caused by elephants in captivity: an examination of predominant factors', *International Zoo Yearbook*, 40: 51–62.

Gosling, S. (2001) 'From mice to men: what can we learn about personality from animal research?', *Psychological Bulletin*, 127: 45–86.

Graczyk, T. K., Cranfield, M. R., Brossy, J. J., Cockrem, J. F., Jouventin, P., and Seddon, P. J. (1995) 'Detection of avian malaria infections in wild and captive penguins', *Journal of the Helminth Society (Washington)*, 62: 135–41.

Graffam, W. S., Irlbeck, N. A., Grandin, T., Mallinckrodt, C., Cambre, R. C., and Phillips, M. (1995) 'Determination of vitamin E status and supplementation for nyala (*Tragelaphus angasi*)', available online at **http://www.nagonline. net/Proceedings/NAG1995/Determination%20of%20 Vitamin%20E%20Status...Nyala.pdf**.

Graham, S. (1996) 'Issues of surplus animals', in D. G. Kleiman, M. E. Allen, K. V. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago, pp. 290–6.

Grand A. P., Kuhar, C. W., Leighty, K. A., Bettinger, T. L., and Laudenslager, M. L. (2012) 'Using personality ratings and cortisol to characterize individual differences in African elephants (*Loxodonta africana*)', *Applied Animal Behaviour Science*, 142: 69–75.

Grandin, T. (2000) 'Habituating antelope and bison to cooperate with veterinary procedures', *Journal of Applied Animal Welfare Science*, 3: 253–61.

Grech, K. S. (2004) 'Brief summary of the laws pertaining to zoos', Animal Legal and Historical Center, Michigan State University College of Law, available online at **http://www.animallaw.info/articles/qvuszoos.htm**.

Greenwood, A. (2003) 'Pox disease in all taxa', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 737–41.

Gregory, N. (2004) *Physiology and Behaviour of Animal Suffering*, Oxford: Blackwell Science.

Griffin, A. S., Blumstein, D. T., and Evans, C. S. (2000) 'Training captive-bred or translocated animals to avoid predators', *Conservation Biology*, 14: 1317–26.

Griffin, A. S., Savani, R., Hausmanis, K., and Lefebvre, L. (2005) 'Mixed species aggregations in birds: zenaida doves, *Zenaida aurita*, respond to the alarm calls of carib grackles, *Quiscalus lugubris*', *Animal Behaviour*, 70: 507–15.

Griffin, D. R. (1992) *Animal Minds*, Chicago, IL: University of Chicago Press.

Grigor, P. N., Hughes, B. O., and Appleby, M. C. (1995) 'Effects of regular handling and exposure to an outside area on subsequent fearfulness and dispersal in domestic hens', *Applied Animal Behaviour Science*, 44: 47–55.

Grim, K. C., McCutchan, T., Li, J., et al. (2004) 'Preliminary results of an anticircumsporozoite DNA vaccine trial for protection against avian malaria in captive African black-footed penguins', *Journal of Zoo and Wildlife Medicine*, 35: 154–61.

Guilarte, T. R., Toscano, C. D., McGlothan, J. L., and Weaver, S. A. (2003) 'Environmental enrichment reverses cognitive and molecular deficits induced by developmental lead exposure', *Annals of Neurology*, 53: 50–6.

Gusset, M. and Dick, G. (2011). The global reach of zoos and aquariums in visitor numbers and conservation expenditures. *Zoo Biology*, 30: 566–9.

Gwynne, J. A. (2007) 'Inspiration for conservation: moving audiences to care', in A. Zimmerman, M. Hatchwell, L. Dickie, and C. West (eds), *Zoos in the 21st Century: Catalysts for Conservation*?, Cambridge: Cambridge University Press, pp. 51–62.

H

Habib, B. and Kumar, S. (2007) 'Den shifting by wolves in semi-wild landscapes in the Deccan Plateau, Maharashtra, India', *Journal of Zoology*, 272: 259–65.

Hadfield, C. (2012) 'Quarantine of fish and aquatic invertebrates in public display aquaria', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Elsevier Saunders, pp. 202–9.

Hadley, C., Hadley, B., Ephraim, S., Yang, M., and Lewis, M. H. (2006) 'Spontaneous stereotypy and environmental enrichment in deer mice (*Peromyscus maniculatus*): reversibility of experience', *Applied Animal Behaviour Science*, 97: 312–22.

Hagenbeck, C. (1909) *Beasts and Men: Being Carl Hagenbeck's Experiences for Half a Century among Wild Animals* (abridged), H. S. R. Elliot and A. G. Thacker (trans.), London: Longmans.

Hahn, E. (1968) *Zoos*, London: Secker & Warburg.

Haig, S. M. (1998) 'Molecular contributions to conservation', *Ecology*, 79: 413–25.

Håkansson, J., Jensen H. J., and Jensen, J. P. (2008) 'A longitudinal study of antipredator behaviour in four successive generations of two populations of captive red junglefowl', *Applied Animal Behaviour Science,* 114: 3–4, 409–18.

Halachmi, I., Edan, Y., Maltz, E., Peiper, U. M., Moallem, U., and Brukental, I. (1998) 'A real-time control system for individual dairy cow food intake', *Computers and Electronics in Agriculture*, 20: 131–44.

Halbrooks, R. D., Swango, L. J., Schnurennberger, P. R., Mitchell, F. E., and Hill, E. P. (1981) 'Response of gray foxes to modified live-virus canine distemper vaccines', *Journal of the American Veterinary Medical Association*, 179: 1170–4.

Halliday, T. (1978) *Vanishing Birds: Their Natural History and Conservation*, London: Sidgwick & Jackson.

Halver, J. E. and Hardy, W. (2002) *Fish Nutrition*, London: Academic Press.

Hamburger, L. (1988) 'Introduction of two young orang-utans *Pongo pygmaeus* into an established family group', *International Zoo Yearbook*, 27: 273–8.

Hamilton, W. D. (1964) 'The genetical evolution of social behaviour', *Journal of Theoretical Biology*, 7: 1–52.

Hammerson, G. and Phillips, C. (2004) '*Cryptobranchus alleganiensis*', in *2006 IUCN Red List of Threatened Species*, available online at **http://iucnredlist.org**.

Hammerstrom, F. (1970) *An Eagle in the Sky*, Ames, IA: Iowa State University Press.

Hancocks, D. (1995) 'Lions and tigers and bears, oh no!', in B. G. Norton, M. Hutchins, E. Stevens, and T. L. Maple (eds), *Ethics on the Ark: Zoos, Animal Welfare and Wildlife Conservation*, Washington, DC: Smithsonian Institute Press, pp. 31–7.

Hancocks, D. (2001) *A Different Nature: The Paradoxical World of Zoos and Their Uncertain Future*, Berkeley, CA: University of California Press.

Hancocks, D. (2012) 'Beyond the animal: exhibiting and interpreting nature', *Proceedings: The Future of Zoos*, available online at **http://www.canisiusishar.org/symposia/future_of_zoos.htm**.

Hanna, J. (1996) 'Ambassadors of the wild', in M. Nichols (ed.), *Keepers of the Kingdom: The New American Zoo*, New York: Thomasson-Grant and Lickle, pp. 75–82.

Hansen, L. T. and Berthelsen, H. (2000) 'The effect of environmental enrichment on the behaviour of caged rabbits (*Oryctolagus cuniculus*)', *Applied Animal Behaviour Science*, 68: 163–78.

Hansen, S. J. and Møller, S. H. (2001) 'The application of a temperament test to on-farm selection of mink', *Acta Agriculturae Scandinavica Section A: Animal Sciences*, 51 (Supplement): 93–8.

Hanson, B., Miller-Klein, P. E., and Melfi, V. (2012) 'I can't hear you! Rethinking the zoo's acoustic environment', in *Proceedings of the World Association of Zoos and Aquaria (WAZA) Annual General Meeting*, Melbourne, Australia (2012) (abstract).

Hanson, E. (2002) *Animal Attractions: Nature on Display in American Zoos*, Princeton, NJ: Princeton University Press.

Harbone, J. B. (1991) 'The chemical basis of plant defense', in R. T. Palo and C. T. Robbins (eds), *Plant Defense Against Mammalian Herbivores*, Boca Raton, FL: CRC Press, pp. 45–60.

Harding, E. J., Paul E. S., and Mendl, M. (2004) 'Animal behaviour: cognitive bias and affective state', *Nature*, 427: 312

Hare, V. J. (2008) 'Enrichment gone wrong!', in Hare, V. J. (ed.) *Proceedings of the Eighth International Conference on Environmental Enrichment*, San Diego, CA: The Shape of Enrichment.

Hare, V. J. and Sevenich, M. (1999) 'Is it training or is it enrichment?', in V. J. Hare, K. E. Worley, and K. Myers (eds), *Proceedings of the Fourth Conference on Environmental Enrichment*, San Diego, CA: The Shape of Enrichment, pp. 40–7.

Hare, V. J., Ripsky, D., Battershill, R., Bacon, K., Hawk, K., and Swaisgood, R. R. (2003) 'Giant panda enrichment: meeting everyone's needs', *Zoo Biology*, 22: 401–16.

Harri, M., Mononen, J., Ahola, L., Plyusnina, L., and Rekliä, T. (2003) 'Behavioural and physiological differences between silver foxes selected and not selected for domestic behaviour', *Animal Welfare*, 12: 305–14.

Harris, L. D., Custer, L. B., Soranaka, E. T., Burge, J. R., and Ruble, G. R. (2001) 'Evaluation of objects and food for environmental enrichment of NZW rabbits', *Contemporary Topics in Laboratory Animal Science*, 40: 27–30.

Harris, M., Sherwin, C., and Harris, S. (2008) *The Welfare, Housing and Husbandry of Elephants in Zoos*, available online at **http://randd.defra.gov.uk**.

Harrison, R., Ford, S., Young, J., Conley, A., and Freeman, A. (1990) 'Increased milk production versus reproductive and energy status of high-producing dairy cows', *Journal of Dairy Science*, 73: 2749–58.

Harvey, N. C., Farabaugh, S. M., and Druker, B. B. (2002) 'Effects of early rearing experience on adult behavior and nesting in captive Hawaiian crows (*Corvus hawaiiensis*)', *Zoo Biology*, 21: 59–75.

Hastings, B. E., Lowenstine, L. J., and Foster, J. W. (1991) 'Mountain gorillas and measles: ontogeny of a wildlife vaccination program', in R. E. Junge (ed.), *Proceedings of the Annual Meeting of the American Association of Zoo Veterinarians*, Yulee, FL: AAZV, pp. 198–205.

Hatchwell, M., Rübel, A., Dickie, L. A., West, C., and Zimmermann, A. (2007) 'Conclusion: the future of zoos', in A. Zimmerman, M. Hatchwell, L. Dickie, and C. West (eds), *Zoos in the 21st Century: Catalysts for Conservation?*, Cambridge: Cambridge University Press, pp. 343–60.

Hatt, J-.M. (2007) 'Raising giant tortoises', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (6th edn), St Louis, MO: Saunders Elsevier, pp. 144–53.

Hatt, J. M. and Clauss, M. (2001) 'Browse silage in zoo animal nutrition: feeding enrichment of browsers during winter', in *Abstract Book, Second European Zoo Nutrition Conference*.

Hawkins, C. E., Baars, C., Hesterman, H., *et al.* (2006) 'Emerging disease and population decline of an island endemic, the Tasmanian devil *Sarcophilus harrisii*', *Biological Conservation*, 131: 307–24.

Hawkins, D. M. (2009). *Biomeasurement: a student's guide to biological statistics* (2nd edn). Oxford: Oxford University Press.

Hawkins, M. and Battaglia, A. (2009). Breeding behaviour of the platypus (*Ornithorhynchus anatinus*) in captivity. *Australian Journal of Zoology*, 57: 283–93.

Hayward, J. and Rothenberg, M. (2004) 'Measuring success in the "Congo Gorilla Forest" conservation exhibition', *Curator*, 47: 261–82.

Hayward, M. W. and Kerley, G. I. H. (2005) 'Prey preferences of lions (*Panthera leo*)', *Journal of Zoology*, 267: 309–22.

Hebb, D. O. (1947) 'The effects of early experience on problem solving at maturity', *American Psychology*, 2: 306.

Hediger, H. (1950) *Wild Animals in Captivity* (trans.), London: Butterworth Scientific Publications.

Hediger, H. (1955) *Psychology of Animals in Zoos and Circuses*, London: Butterworth Scientific Publications.

Hediger, H. (1965) 'Man as a social partner of animals and vice versa', *Symposia of the Zoological Society of London*, 14: 291–300.

Hediger, H. (1970) *Man and Animal in the Zoo*, London: Routledge & Kegan Paul.

Heldman, D. R. (ed.) (2003) *Encyclopedia of Agricultural, Food, and Biological Engineering*, New York: Marcel Dekker.

Heleski, C. R. and Zanella, A. J. (2006) 'Animal science student attitudes to farm animal welfare', *Anthrozoös*, 19: 3–16.

Hellmuth, H., Augustine, L., Watkins, B., and Hope, K. (2012) 'Using operant conditioning and desensitization to facilitate veterinary care with captive reptiles', *Veterinary Clinics of North America: Exotic Animal Practice*, 15: 425–43.

Hemdal, J. (2006) *Advanced Marine Aquarium Techniques*, Neptune City, NJ: TFH Publications.

Hemsworth, P. H. (2003) 'Human–animal interactions in livestock production', *Applied Animal Behaviour Science*, 81: 185–98.

Henderson, J. V. and Waran, N. K. (2001) 'Reducing equine stereotypies using an Equiball™', *Animal Welfare*, 10: 73–80.

Herbert, P. and Bard, K. (2000) 'Orang-utan use of vertical space in an innovative habitat', *Zoo Biology*, 19: 239–51.

Herrnstein, R. J. (1979) 'Acquisition, generalization, and discrimination reversal of a natural concept', *Journal of Experimental Psychology: Animal Behaviour Processes*, 5: 116–29.

Hesterman, H., Gregory, N., and Boardman, W. (2001) 'Deflighting procedures and their welfare implications in captive birds', *Animal Welfare*, 10: 405–19.

Hiby, E. F., Rooney, N. J., and Bradshaw, J. W. S. (2006) 'Behavioural and physiological responses of dogs entering re-homing kennels', *Physiology and Behavior*, 89: 385–91.

Hildebrandt, T., Göritz, F., and Hermes, R. (2006) 'Ultrasonography: an important tool in captive breeding management in elephants and rhinoceroses', *European Journal of Wildlife Research*, 52: 23–7.

Hill, G. and Sharp, A. (2010) *Zoo Research Guidelines: Aquarium Based Research*, London: BIAZA.

Hill, S. P. (2009) 'Do gorillas regurgitate potentially-injurious stomach acid during "regurgitation and reingestion"?', *Animal Welfare* 18: 123–27.

Hinshaw, K. C., Amand, W. B., and Tinkelman, C. L. (1996) 'Preventive medicine', in D. G. Kleiman, M. E. Allen, K. V. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago Press, pp. 16–24.

HMSO (2002) *The Zoo Licensing Act 1981 (Amendment) (England and Wales) Regulations 2002*, SI 2002/3080 (© Crown Copyright 2002), London: Her Majesty's Stationery Office.

Hoage, R. J., and Deiss, W. A. (1996) *New Worlds, New Animals: From Menagerie to Zoological Park in the Nineteenth Century*, Baltimore, MD: Johns Hopkins University Press.

Hoff, M. P., Powell, D. M., Lukas, K. E., and Maple, T. L. (1997) 'Individual and social behaviour of lowland gorillas in outdoor exhibits compared with indoor holding areas', *Applied Animal Behaviour Science*, 54: 359–70.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., *et al.* (2010). The impact of conservation on the status of the world's vertebrates. *Science NY*, 330: 1503–9.

Hogan, E. S., Houpt, K. A., and Sweeney, K. (1988) 'The effect of enclosure size on social interactions and daily activity patterns of the captive Asiatic wild horse (*Equus przewalskii*)', *Applied Animal Behaviour Science*, 21: 147–68.

Hogan, L. A. and Tribe, A. (2007) 'Prevalence and cause of stereotypic behaviour in common wombats (*Vombatus ursinus*) residing in Australian zoos', *Applied Animal Behaviour Science*, 105: 180–91.

Hogan, L. A., Johnston, S. D., Lisle, A. T., et al. (2012) 'Behavioural and physiological responses of captive wombats (*Lasiorhinus latifrons*) to regular handling by humans', *Applied Animal Behaviour Science*, 134: 217–28.

Hogg, C. J., Hibbard, C., Ford, C., and Embury, A (2012) 'Species management benchmarking: outcomes over outputs in a changing operating environment', *Zoo Biology*, doi: 10.1002/zoo.21039 [Epub ahead of print].

Höhn, M., Kronschnabel, M., and Ganslosser, U. (2000) 'Similarities and differences in activities and agonistic behaviour of male Eastern grey kangaroos (*Macropus giganteus*) in captivity and the wild', *Zoo Biology*, 19: 529–39.

Holst, B., and Dickie, L. A. (2007) 'How do national and international regulations and policies influence the role of zoos and aquariums in conservation?', in A. Zimmerman, M. Hatchwell, L. Dickie, and C. West (eds), *Zoos in the 21st Century: Catalysts for Conservation?*, Cambridge: Cambridge University Press, pp. 22–33.

Holt, W., Pickard, A., Rodger, J., and Wildt, D. (eds) (2003) *Reproductive Science and Integrated Conservation*, Cambridge: Cambridge University Press.

Holzer, D. and Scott, D. (1997) 'The long-lasting effects of early zoo visits', *Curator*, 40: 255–7.

Honess, P. E. and Marin, C. M. (2006) 'Enrichment and aggression in primates', *Neuroscience and Biobehavioral Reviews*, 30: 413–36.

Honess, P. E., Johnson, P. J., and Wolfensohn, S. E. (2004) 'A study of behavioural responses of non-human primates to air transport and re-housing', *Laboratory Animals*, 38: 119–32.

Hooper, K. J. and Newsome, J. T. (2004) 'Proactive compliance: the team program approach to revitalizing primate enrichment', *Contemporary Topics*, 43: 37–8.

Hope, K. and Deem, S. L. (2006) 'Retrospective study of morbidity and mortality of captive jaguars (*Panthera onca*) in North America: 1982–2002', *Zoo Biology*, 25: 501–12.

Hörnicke, H. (1981) 'Utilization of caecal digesta by caecotrophy (soft faeces ingestion) in the rabbit', *Livestock Production Science*, 8: 361–6.

Horwich, R. H. (1989) 'Use of surrogate parental models and age periods in a successful release of hand-reared sandhill cranes', *Zoo Biology*, 8: 379–90.

Hosey, G. R. (1989) 'Behavior of the Mayotte lemur, *Lemur fulvus mayottensis*, in captivity', *Zoo Biology*, 8: 27–36.

Hosey, G. R. (1997) 'Behavioural research in zoos: academic perspectives', *Applied Animal Behaviour Science*, 51: 199–207.

Hosey, G. R. (2000) 'Zoo animals and their human audiences: what is the visitor effect?', *Animal Welfare*, 9: 343–57.

Hosey, G. R. (2005) 'How does the zoo environment affect the behaviour of captive primates?', *Applied Animal Behaviour Science*, 90: 107–29.

Hosey, G. R. (2008) 'A preliminary model of human–animal relationships in the zoo', *Applied Animal Behaviour Science*, 109: 105–27.

Hosey, G. R. (2013) 'Hediger revisited: how do zoo animals see us?', *Journal of Applied Animal Welfare Science*, in press.

Hosey, G. R. and Druck, P. L. (1987) 'The influence of zoo visitors on the behaviour of captive primates', *Applied Animal Behaviour Science*, 18: 19–29.

Hosey, G. R. and Skyner, L. J. (2007) 'Self-injurious behaviour in zoo primates', *International Journal of Primatology*, 28: 1431–7.

Hosey, G. R. and Melfi, V. A. (2012) 'Human–animal bonds between zoo professionals and the animals in their care', *Zoo Biology*, 31: 13–26.

Hosey, G. R., Jacques, M., and Pitts, A. (1997) 'Drinking from tails: social learning of a novel behaviour in a group of ring-tailed lemurs (*Lemur catta*)', *Primates*, 38: 415–22.

Hosey, G., Hill, S., and Lherbier, M. (2012) 'Can zoo records help answer behavioural research questions? The case of the left-handed lemurs (*Lemur catta*)', *Zoo Biology*, 31: 189–96.

Houts, L. (1999) 'Supplemental carcass feeding for zoo carnivores', *The Shape of Enrichment*, 8: 1–3.

Howard, B. R. (1992) 'Health risks of housing small psittacines in galvanized wire mesh cages', *Journal of American Veterinary Medical Association*, 235: 469–83.

Howard, J. and Allen, M. E. (2007) 'Nutritional factors affecting semen quality in felids', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (6th edn), St Louis, MO: Saunders Elsevier, pp. 272–83.

Howell, S., Matevia, M., Fritz, J., Nash, L., and Maki, S. (1993) 'Pre-feeding agonism and seasonality in captive groups of chimpanzees (*Pan troglodytes*)', *Animal Welfare*, 2: 153–63.

Hoy, J. M., Murray, P. J., and Tribe, A. (2010) 'The potential for microchip-automated technology to improve enrichment practices', *Zoo Biology*, 29: 586–99.

HSE (Health and Safety Executive) (2006) *Managing Health and Safety in Zoos*, available online at **http:// www.hse.gov.uk/pubns/web15.pdf**.

Hu, H. and Jiang, Z. (2002) 'Trial release of Père David's deer *Elaphurus davidianus* in the Dafeng Reserve, China', *Oryx*, 36: 196–9.

Huber, H. F. and Lewis, K. P. (2011) 'An assessment of gum-based environmental enrichment for captive gummivorous primates', *Zoo Biology* 30: 71–8.

Huffman, M. A. and Hirata, S. (2004) 'An experimental study of leaf swallowing in captive chimpanzees: insights into the origin of a self-medicative behavior and the role of social learning', *Primates*, 45: 113–18.

Hunt, R. D., Garcia, F. G., Hegsted, D. M., and Kaplinsky, N. (1967) 'Vitamins D2 and D3 in New World primates: influence on calcium absorption', *Science*, 157: 943–5.

Hunt, S., Cuthill, I., Swaddle, J., and Bennett, A. (1997) 'Ultraviolet vision and band-colour preferences in female zebra finches, *Taeniopygia guttata*', *Animal Behaviour*, 54: 1383–92.

Hunter, M. L., Jr (1995) *Fundamentals of Conservation Biology*, Oxford: Blackwell Science.

Huntingford, F. and Turner, A. (1987) *Animal Conflict*, London: Chapman & Hall.

Hurme, K., Gonzalez, K., Halvorsen, M., Foster, B., Moore, D., and Chepko-Sade, B. D. (2003) 'Environmental enrichment for dendrobatid frogs', *Journal of Applied Animal Welfare Science*, 6: 285–99.

Hutchins, D. M., Willis, K., and Wiese, R. J. (1995) 'Strategic collection planning: theory and practice', *Zoo Biology*, 14: 5–25.

Hutchins, M. (2001) 'Research: overview', in C. E. Bell (ed.), *Encyclopedia of the World's Zoos*, Chicago, IL/ London: Fitzroy Dearborn, pp. 1076–80.

Hutchins, M. (2006) 'Variation in nature: its implications for zoo elephant management', *Zoo Biology*, 25: 161–71.

Hutchins, M. and Thompson, S. D. (2008) 'Zoo and aquarium research: priority setting for the coming decades', *Zoo Biology*, 27: 488–97.

Hutchins, M. and Wiese, R. (1991) 'Beyond genetic and demographic management: the future of the SSP and related AAZPA conservation efforts', *Zoo Biology*, 10: 285–92.

Hutchins, M., Hancocks, D., and Calip, T. (1978) 'Behavioural engineering in the zoo: a critique', *International Zoo News*, 25: 18–23.

Hutchins, M., Smith, G. M., Mead, D. C., Elbin, S., and Steenberg, J. (1991) 'Social behaviour of Matschie's tree kangaroos (*Dendrolagus matschiei*) and its implications for captive management', *Zoo Biology*, 10: 147–64.

I

IATA (International Air Transport Association) (2012) *Live Animal Regulations*, Montreal: IATA.

ICEE (International Conference on Environmental Education) (2007) *Environmental Education Towards a Sustainable Future: Partners for the Decade of Education for Sustainable Development*, *Fourth International Conference on Environmental Education*, Ahmedabad, India: Centre for Environment Education.

Ickes, B. R., Pham, T. M., Sanders, L. A., Albeck, D. S., Mohammed, A. H., and Granholm, A. C. (2000) 'Long-term environmental enrichment leads to regional increases in neurotrophin levels in rat brain', *Experimental Neurology*, 164: 45–52.

Inglis, I. R. and Ferguson, N. (1986) 'Starlings search for food rather than eat freely-available, identical food', *Animal Behaviour*, 34: 614–17.

Inglis, I. R., Forkman, B., and Lazarus, J. (1997) 'Free food or earned food? A review and fuzzy model of contrafreeloading', *Animal Behaviour*, 53: 1171–91.

Ings, R., Waran, N. K., and Young, R. J. (1997a) 'Attitude of zoo visitors to the idea of feeding live prey to zoo animals', *Zoo Biology*, 16: 343–7.

Ings, R., Waran, N. K., and Young, R. J. (1997b) 'Effect of wood-pile feeders on the behaviour of captive bush dogs (*Speothos venaticus*)', *Animal Welfare*, 6: 145–52.

Isaza, R. (2003) 'Tuberculosis in all taxa', in M. E. Fowler and M. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 689–96.

ISIS (International Species Information System) (2004) *User Manual for SPARKS: Single Population Analysis and Records Keeping System Version 1.5*, Eagen, MN: ISIS.

IUCN (International Union for the Conservation of Nature and Natural Resources) (2006) *Red Data List of Threatened Species*, available online at **http://www. iucnredlist.org** (accessed June 2007).

IUCN (International Union for the Conservation of Nature and Natural Resources) (2007) *Red Data List of Threatened Species*, available online at **http://www.iucnredlist.org** (accessed 20 April 2008).

IUCN (International Union for the Conservation of Nature and Natural Resources) (2012) 'Table 1. Numbers of threatened species by major groups of organisms 1996–2012', *IUCN Red List*, available online at: **http://www.iucnredlist.org/documents/summarystatistics/2012_2_RL_Stats_Table1.pdf** (accessed 30 October 2012).

IUCN/SSC (International Union for the Conservation of Nature and Natural Resources/Species Survival Commission) (1998) *IUCN Guidelines for Re-Introductions*, prepared by the IUCN/SSC Re-introduction Specialist Group, Gland/Cambridge: IUCN.

IUDZG/CBSG (International Union of Directors of Zoological Gardens/Conservation Breeding Specialist Group) (The World Zoo Organisation and the Captive Breeding Specialist Group of the IUCN/SSC) (1993) *The World Zoo Conservation Strategy: The Role of the Zoos and Aquaria of the World in Global Conservation*, Chicago, IL: Chicago Zoological Society.

J

Jackson, D. (1996) 'Horticultural philosophies in zoo exhibit design', in D. Kleiman, M. Allen, K. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago, pp. 175–9.

Jackson, S. (2010) *Australian Mammals: Biology and Captive Management*, Collingwood, Victoria: CSIRO.

Jackson, S. and Wilson, R. P. (2002) 'The potential costs of flipper-bands to penguins', *Functional Ecology*, 16: 141–8.

Jadavji, N. M., Kolb, B., and Metz, G. A. (2006) 'Enriched environment improves motor function in intact and unilateral dopamine-depleted rats', *Neuroscience*, 140: 1127–38.

Jago, N., Dorey, N., and Melfi, V. (2006) 'Training Goeldi's monkeys (*Callimico goeldii*) for weighting and crating', in N. Dorey (ed.) *Proceedings of the Animal Behavior Management Alliance Annual Conference*, pp. 113–15, available online at **http://www.theabma.org**

James, S. B. (2012) 'Children's zoo medicine: zoonoses', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 115–24.

Jamieson, D. (1995) 'Zoos revisited', in B. G. Norton, M. Hutchins, E. Stevens, and T. L. Maple (eds), *Ethics on the Ark: Zoos, Animal Welfare and Wildlife Conservation*, Washington, DC: Smithsonian Institute Press, pp. 52–66.

Jamieson, N. and Portas, T. (no date) 'The sustainable management of ungulate species in the Australasian region: surplus animals and lessons drawn from nature', *Proceedings of ARAZPA AGM.*

Janssen, D. L. (2012) 'Guidelines for the management of zoonotic diseases', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 47–50.

Jenkins, M. (2003) 'Prospects for biodiversity', *Science*, 302: 1175–7.

Jennison, G. (2005) *Animals for Show and Pleasure in Ancient Rome*, Philadelphia, PA: University of Pennsylvania Press.

Jeppesen, L. L., Heller, K. E., and Bildsoe, M. (2004) 'Stereotypies in female farm mink (*Mustela vison*) may be genetically transmitted and associated with higher fertility due to effects on body weight', *Applied Animal Behaviour Science*, 86: 137–43.

Johnson, A. J., Pessier, A. P., Wellehan, J. F. X., Brown, R., and Jacobson, E. R. (2005) 'Identification of a novel herpesvirus from a California desert tortoise (*Gopherus agassizii*)', *Veterinary Microbiology*, 111: 107–16.

Johnson, L. (2000) 'Sexing mammalian sperm for production of offspring: the state-of-the-art', *Animal Reproduction Science*, 60/61: 93–107.

Jones, G., Coe, J., and Paulson, D. (1976) *Long-Range Plan for Woodland Park Zoological Gardens*, Seattle, WA: Jones & Jones for the Seattle Department of Parks and Recreation.

Jones, M. and Pillay, N. (2004) 'Foraging in captive hamadryas baboons: implications for enrichment', *Applied Animal Behaviour Science*, 88: 101–10.

Jones, M. E., Jarman, P. J., Lees, C. M., *et al.* (2007) 'Conservation management of Tasmanian devils in the context of an emerging, extinction-threatening disease: devil facial tumour disease', *EcoHealth*, 4: 326–37.

Jones, T. A., Hawrylak, N., Klintsova, A. Y., and Greenough, W. T. (1998) 'Brain damage, behavior, rehabilitation, recovery, and brain plasticity', *Mental Retardation and Developmental Disabilities Research Reviews*, 4: 231–7.

Judge, P. G. and de Waal, F. B. M. (1997) 'Rhesus monkey behaviour under diverse population densities: coping with long-term crowding', *Animal Behaviour*, 54: 643–62.

Jule, K. R., Leaver, L. A., and Lea, S. E. G. (2008) 'The effects of captive experience on reintroduction survival in carnivores: a review and analysis', *Biological Conservation*, 141: 355–63.

K

Kaandorp, J. (2012) 'Veterinary challenges of mixed species exhibits', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 24–31.

Kagan, R. and Veasey, J. (2010) 'Challenges of zoo animal welfare', in D. G. Kleiman, K. V. Thompson, and C. Kirk Baer (eds), *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: University of Chicago Press, pp. 11–21.

Kalk, P. and Rice, C. G. (2010) 'Identification and marking techniques', in D. G. Kleiman, K. V. Thompson, and C. Kirk Baer (eds), *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: University of Chicago Press, pp. 493–503.

Kapos, V., Balmford, A., Aveling, R., et al. (2009) 'Outcomes, not implementation, predict conservation success', *Oryx* 43: 336–42.

Kawai, M. (1965) 'Newly-acquired precultural behavior of the natural troop of Japanese monkeys on Koshima Islet', *Primates*, 6: 1–30.

Kawakami, K., Takeuchi, T., Yamaguchi, S., et al. (2003) 'Preference of guinea pigs for bedding materials: wood shavings versus paper cutting sheet', *Experimental Animals*, 52: 11–15.

Keane, C. and Marples, N. (2003) 'The effects of zoo visitors on gorilla behaviour', in T. C. Gilbert (ed.), *Proceedings of the Fifth Annual Symposium on Zoo Research*, London: BIAZA, pp. 144–54.

Keeling, C. H. (1984) *Where the Lion Trod: A Study of Forgotten Zoological Gardens*, London: Clam Productions.

Kellert, S. (1979) 'Zoological parks in American society', in *AAZPA Annual Proceedings*, Wheeling, WV: AAZPA, pp. 88–126.

Kelley, J. L. and Magurran, A. E. (2006) 'Captive breeding promotes aggression in an endangered Mexican fish', *Biological Conservation*, 133: 169–77.

Kerridge, F. J. (1996) 'Behavioural enrichment of ruffed lemurs (*Varecia variegata*) based upon a wild–captive comparison of their behaviour', PhD thesis, University of Manchester (Bolton Institute).

Kerridge, F. J. (2005) 'Environmental enrichment to address behavioral differences between wild and captive black-and-white ruffed lemurs (*Varecia variegata*)', *American Journal of Primatology*, 66: 71–84.

Kertesz, P. (1993) *A Colour Atlas of Veterinary Dentistry and Oral Surgery*, London: Wolfe.

Kesler, D., Lopes, I., and Haig, S. (2006) 'Sex determination of Pohnpei Micronesian Kingfishers using morphological and molecular genetic techniques', *Journal of Field Ornithology*, 77: 229–32.

Ketz-Riley, C. J. (2003) 'Salmonellosis and shigellosis', in M. E. Fowler and M. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 686–9.

Kierulff, M. C. M., Ruiz-Miranda, C. R., de Oliviera, P., et al. (2012) 'The golden lion tamarin *Leontopithecus rosalia*: a conservation success story', *International Zoo Yearbook*, 46: 36-45.

Kiley-Worthington, M. (1989) 'Ecological, ethological, and ethically sound environments for animals: towards symbiosis', *Journal of Agricultural Ethics*, 2: 323–47.

Kilner, R. (1998) 'Primary and secondary sex ratio manipulation by zebra finches', *Animal Behaviour*, 56: 155–64.

Kim, R., Eggeling, H., and Ruster, W (2010) *The Socio-economic Impact of Members of the European Association of Zoos and Aquaria.* Amsterdam: EAZA Executive Office.

Kinkel, L. (1989) 'Lasting effects of wing tags on ring-billed gulls', *Auk*, 106: 619–24.

Kirk Baer, C., Ullrey, D. E., Schlegel, M. L., Agoramoorthy, G, and Baer, D. J. (2010). 'Contemporary topics in wild mammal nutrition', in D. G. Kleiman, K. V. Thompson, and C. Kirk Baer (eds), *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: University of Chicago Press, pp. 85–103.

Kirkwood, J. K. (2001a) 'United Kingdom: legislation', in C. E. Bell (ed.), *Encyclopedia of the World's Zoos*, Chicago, IL/London: Fitzroy Dearborn, pp. 1281–3.

Kirkwood, J. K. (2001b) 'United Kingdom: licensing', in C. E. Bell (ed.), *Encyclopedia of the World's Zoos*, Chicago, IL/London: Fitzroy Dearborn, pp. 1284–5.

Kirkwood, J. K. and Cunningham, A. A. (1994) 'Epidemiologic observations on spongiform encephalopathies in captive wild animals in the British Isles', *Veterinary Record*, 135: 296–303.

Kirkwood, J. K., Wells., G. A. H., Wilesmith, J. W., Cunningham, A. A., and Jackson, S. I. (1990) 'Spongiform encephalopathy in an Arabian oryx (*Oryx leucoryx*) and a greater kudu (*Tragelaphus strepsiceros*)', *Veterinary Record*, 127: 418–20.

Kirkwood, J. K., Cunningham, A. A., Flach, E. J., Thornton, S. M., and Wells, G. A. H. (1995) 'Spongiform encephalopathy in another captive cheetah (*Acinonyx jubatus*): evidence for variation in susceptibility or incubation periods between species?', *Journal of Zoo and Wildlife Medicine*, 26: 577–82.

Kisling, V. N. (2001) *Zoo and Aquarium History: Ancient Animal Collections to Zoological Gardens*, Boca Raton, FL: CRC Press.

Kitchener, A. C. and Macdonald, A. (2004) 'The longevity legacy: the problem of old mammals in zoos', in B. Hiddinga (ed.), *Proceedings of the EAZA Conference*, Amsterdam: EAZA Executive Office, pp. 132–7.

Klasing, K. C. (1998) *Comparative Avian Nutrition*, Wallingford, Oxon: CABI Publishing.

Kleiman, D. G. (1992) 'Behavior research in zoos: past, present and future', *Zoo Biology*, 1110: 301–12.

Kleiman, D. G. (1994) 'Animal behavior studies and zoo propagation programs', *Zoo Biology*, 1310: 411–12.

Kleiman, D. G., Beck, B. B., Dietz, J. M., Dietz, L. A., Ballou, J. D., and Coimbra-Filho, A. C. (1986) 'Conservation program for the golden lion tamarins: captive research and management, ecological studies, educational strategies and reintroduction', in K. Benirschke (ed.), *Primates: The Road to Self-Sustaining Populations*, New York: Springer, pp. 959–79.

Kleiman, D. G., Beck, B. B., Dietz, J. M., and Dietz, L. A. (1991) 'Costs of reintroduction and criteria for success: accounting and accountability in the golden lion tamarin conservation program', in J. H. W. Gipps (ed.) 'Beyond captive breeding: re-introducing endangered animals to the wild', *Symposium of the Zoological Society of London*, 62: 125–42.

Kleiman, D. G., Stanley Price, M. R., and Beck, B. B. (1994) 'Criteria for reintroductions', in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner (eds), *Creative Conservation: Interactive Management of Wild and Captive Animals*, London: Chapman & Hall, pp. 287–303.

Kleiman, D. G., Allen, M. E., Thompson, K. V., and Lumpkin, S. (eds) (1996) *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago Press.

Kleiman, D. G., Thompson, K. V., and Kirk Baer, C. (2010) *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: Chicago University Press.

Knight, K., Pearson, R., and Melfi, V. (2005) 'Does the provision of carcasses compromise the health of zoo-housed carnivores?', in A. Nicklin (ed.) *Proceedings of the Seventh Annual BIAZA Research Meeting*, London: BIAZA, pp. 194–8.

Knowles, J. M. (1985) 'Wild and captive populations: triage, contraception and culling', *International Zoo Yearbook*, 24–25: 206–10.

Koene, P. and Duncan, I. J. H. (2001) 'From environmental requirement to environmental enrichment: from animal suffering to animal pleasure', in M. Hawkins (ed.), *Proceedings of the Fifth Annual Conference on Environmental Enrichment*, San Diego, CA: The Shape of Enrichment, p. 36.

Kohn, B. (1994) 'Zoo animal welfare', *Revue Scientifique et Technique de l'Office International Des Epizooties*, 13: 233–45.

Koldewey, H. J., Atkinson, J., and Debney, A. (2009). Threatened species on the menu? Towards sustainable seafood use in zoos and aquariums. *International Zoo Yearbook*, 43: 71–81.

Kolter, N. and Kolter, P. (1998) *Museum Strategy and Marketing: Designing Missions, Building Audiences, Generating Revenue and Resources*, San Francisco, CA: Jossey-Bass.

Korte, S. M., Olivier, B., and Koolhaas, J. M. (2007) 'A new animal welfare concept based on allostasis', *Physiology and Behavior*, 92: 422–8.

Koutsos, E. A., Armstrong, D., Ball, R., *et al.* (2011) 'Influence of diet transition on serum calcium and phosphorus and fatty acids in zoo giraffe (*Giraffa camelopardalis*)', *Zoo Biology* 30: 523–31.

Kratochvil, H. and Schwammer, H. (1997) 'Reducing acoustic disturbances by aquarium visitors', *Zoo Biology*, 16: 349–53.

Krebs, J. R., Davies, N. B., and West, S. A. (2012) *An Introduction to Behavioural Ecology* (4th edn), Chichester: Wiley–Blackwell.

Kreger, M. D. and Hutchins, M. (2010) 'Ethics of keeping mammals in zoos and aquariums', in D. G. Kleiman, K. V. Thompson, and C. Kirk Baer (eds), *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: University of Chicago Press, pp. 3–10.

Kreger, M. D. and Mench, J. A. (1995) 'Visitor–animal interactions at the zoo', *Anthrozoös*, 8: 143–58.

Kuhar, C. W. (2006) 'In the deep end: pooling data and other statistical challenges in zoo and aquarium research', *Zoo Biology*, 25: 339–52.

Kuhar, C. W. (2008) 'Group differences in captive gorillas' reaction to large crowds', *Applied Animal Behaviour Science*, 110: 377–85.

Kuhar, C. W., Bettinger, T., and Laudenslager, M. (2005) 'Salivary cortisol and behaviour in an all-male group of western lowland gorillas (*Gorilla g. gorilla*)', *Animal Welfare*, 14: 187–93.

Kuhar, C. W., Stoinski, T. S., Lukas, K. E., and Maple, T. L. (2006) 'Gorilla Behavior Index revisited: age, housing and behavior', *Applied Animal Behaviour Science*, 96: 315–26.

Kuhar, C. W., Miller, L. J., Lehnhardt, J., Christman, J., Mellen, J. D., and Bettinger, T. L. (2010) 'A system for monitoring and improving animal visibility and its implications for zoological parks', *Zoo Biology*, 29: 68–79.

Kurth, A. and Nitsche, A. (2012) 'Cowpox in zoo animals', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 32–7.

Kusuda, S., Ikoma, M., Morikaku, K., *et al.* (2007) 'Estrous cycle based on blood progesterone profiles and changes in vulvar appearance in Malayan tapirs (*Tapirus indicus*)', *Journal of Reproduction and Development*, 53: 1283–9.

Kutska, D. (2009) 'Variation in visitor perceptions of a polar bear enclosure based on the presence of natural vs un-natural enrichment items', *Zoo Biology*, 28: 292–306.

Kyle, D. G. (2001) *Spectacles of Death in Ancient Rome*, London: Routledge.

L

Lacy, R. C. (2013) 'Achieving true sustainability of zoo populations', *Zoo Biology*, 32: 19–26.

Ladewig, J. (1987) 'Endocrine aspects of stress: evaluation of stress reactions in farm animals', in P. Wiepkema and P. van Adrichem (eds), *Biology of Stress in Farm Animals: An Integrative Approach*, Dordrecht: Martinus Nijhoff, pp. 13–25.

Laikre, L. (1999) 'Conservation genetics of Nordic carnivores: lessons from zoos', *Hereditas*, 130: 203–16.

Laikre, L. and Ryman, N. (1991) 'Inbreeding depression in a captive wolf (*Canis lupus*) population', *Conservation Biology*, 5: 33–40.

Lair, S., Barker, I. K., Mehren, K. G., and Williams, E. S. (2002) 'Epidemiology of neoplasia in captive black-footed ferrets (*Mustela nigripes*) 1986–1996', *Journal of Zoo and Wildlife Medicine*, 33: 204–13.

Lamb, M. E. and Hwang, C. P. (1982) 'Maternal attachment and mother–neonate bonding: a critical review', in M. E. Lamb and A. L. Brown (eds), *Advances in Developmental Psychology*, Hillsdale, NJ: Laurence Erlbaum, pp. 1–39.

Lamberski, N. (2003) 'Psittaciformes (parrots, macaws, lories)', in M. E. Fowler and M. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 187–210.

Lamberski, N. (2012) 'Updated vaccination recommendations for Carnivores', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 442–50.

Lamikanra, O., Imam, S. H., and Ukuku, D. (2005) *Produce Degradation*, Boca Raton, FL: CRC Press.

Langkilde, T. and Shine, R. (2006) 'How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*', *Journal of Experimental Biology*, 209: 1035–43.

Landolfi, J. A., Baktiar, O. K., Poynton, S. L., and Mankowski, J. L. (2003) 'Hepatic *Calodium hepaticum* (Nematoda) infection in a zoo colony of black-tailed prairie dogs (*Cynomys ludovicianus*)', *Journal of Zoo and Wildlife Medicine*, 34: 371–4.

Lane, J. (2006) 'Can non-invasive glucocorticoid measures be used as reliable indicators of stress in animals?', *Animal Welfare*, 15: 331–42.

Langan, J. N. (2012) 'Integrated pest management', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 51–9.

Lanza, R. P., Cibelli, J. B., Diaz, F., *et al.* (2000) 'Cloning of an endangered species (*Bos gaurus*) using interspecies nuclear transfer', *Cloning*, 2: 9–90.

Latham, N. R. and Mason, G. J. (2008) 'Maternal deprivation and the development of stereotypic behaviour', *Applied Animal Behaviour Science*, 110: 84–108.

Lauer, J. (1976) *Saqqara: The Royal Cemetery of Memphis, Excavations and Discoveries since 1850*, London: Thames & Hudson.

Laule, G. E. and Desmond, T. (1998) 'Positive reinforcement training as an enrichment strategy', in D. J. Shepherdson, J. D. Mellen, and M. Hutchins (eds), *Second Nature: Environmental Enrichment for Captive Animals*, Washington, DC: Smithsonian Institution Press, pp. 302–13.

Laule, G. E., Bloomsmith, M. A., and Schapiro, S. J. (2003) 'The use of positive reinforcement training techniques to enhance the care, management, and welfare of primates in the laboratory', *Journal of Applied Animal Welfare Science*, 6: 163–73.

Laurenson, M. (1993) 'Early maternal behavior of wild cheetahs: implications for captive husbandry', *Zoo Biology*, 12: 31–43.

Lay, D. C., Jr, Friend, T. H., Bowers, C. L., Grissom, K. K., and Jenkins, O. C. (1992) 'A comparative physiological and behavioral study of freeze and hot-iron branding using dairy cows', *Journal of Animal Science*, 70: 1121–5.

Leader-Williams, N., Balmford, A., Linkie, M., *et al.* (2007) 'Beyond the ark: conservation biologists' views of the achievements of zoos in conservation', in A. Zimmerman, M. Hatchwell, L. Dickie, and C. West (eds), *Zoos in the 21st Century: Catalysts* Cambridge: Cambridge University Press, pp. 236–54.

Le Boeuf, B. J. (1974) 'Male–male competition and reproductive success in elephant seals', *American Zoology*, 14: 163–76.

Leck, C. (1980) 'Establishment of new population centers with changes in migration patterns', *Journal of Field Ornithology*, 51: 168–73.

Lee, T., Burch, J. B., Coote, T., *et al.* (2009) 'Moorean tree snail survival revisited: a multi-island genealogical perspective', *BMC Evolutionary Biology*, 9: 204.

Lees, C. (1993) 'Managing harems in captivity: the Sulawesi crested macaque (*Macaca nigra*)', MSc dissertation, University of Kent, Canterbury.

Lees, C. M. and Wilcken, J. (2009) 'Sustaining the ark: the challenges faced by zoos in maintaining viable populations', *International Zoo Yearbook*, 43: 6–18.

Lees, C. M., and Wilcken, J. (2011) 'Global programmes for sustainability', *Towards Sustainable Population Management*, 2: 4–7.

Lehner, P. N. (1998) *Handbook of Ethological Methods* (2nd edn), Cambridge: Cambridge University Press.

Leipold, H. W. (1980) 'Congenital defects of zoo and wild mammals: a review', in R. J. Montali and G. Migaki (eds), *The Comparative Pathology of Zoo Animals*, Washington, DC: Smithsonian Institute, pp. 457–70.

Lemasson, A., Gautier, J.-P., and Hausberger, M. (2005) 'A brief note on the effects of the removal of individuals on social behaviour in a captive group of Campbell's monkeys (*Cercopithecus campbelli campbelli*): a case study', *Applied Animal Behaviour Science*, 91: 289–96.

Lemm, J., Steward, S., and Schmidt, T. (2005) 'Reproduction of the critically endangered Anegada Island iguana *Cyclura pinguis* at San Diego Zoo', *International Zoo Yearbook*, 39: 141–52.

LeNeindre, P., Boivin, X., and Boissy, A. (1996) 'Handling of extensively kept animals', *Applied Animal Behaviour Science*, 49: 73–81.

Leonardi, R., Buchanan-Smith, H. M., Dufour, V., Macdonald, C., and Whiten, A. (2010) 'Living together: behaviour and welfare in single and mixed species groups of capuchin (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*)', *American Journal of Primatology* 72: 33–47.

Less, E. H., Kuhar, C. W., Dennis, P. M., and Lukas, K. E. (2012) 'Assessing inactivity in zoo gorillas using keeper ratings and behavioural data', *Applied Animal Behaviour Science*, 137: 74–9.

Leus, K. (2006) *EAZA Adaptation of AZA Studbook Analysis and Population Management Handbook*, Amsterdam/Antwerp: EAZA Executive Office/Royal Zoological Society of Antwerp.

Leus, K., Traylor-Holzer, K., and Lacy, R. C. (2011) 'Genetic and demographic population management in zoos and aquariums: recent developments, future challenges and opportunities for scientific research', *International Zoo Yearbook*, 45: 213–25.

Lewis, J. C. M., Fitzgerald, A. J., Gulland, F., *et al.* (1989) 'Observations on the treatment of necrobacillosis in wallabies', *British Veterinary Journal*, 145: 394–6.

Lewke, R. and Stroud, R. (1974) 'Freeze-branding as a method of marking snakes', *Copeia*, 4: 997–1000.

Lindberg, J., Björnerfeldt, S., Saetre, P., *et al.* (2005) 'Selection for tameness has changed brain gene expression in silver foxes', *Current Biology*, 15: 915–16.

Lindburg, D. G. (1988) 'Improving the feeding of captive felines through application of field data', *Zoo Biology*, 7: 211–18.

Line, S., Morgan, K., Markowitz, H., and Strong, S. (1989a) 'Heart rate and activity of rhesus monkeys in response to routine events', *Laboratory Primate Newsletter*, 28: 9–12.

Line, S., Morgan, K., Markowitz, H., and Strong, S. (1989b) 'Influence of cage size on heart rate and behaviour in rhesus monkeys', *American Journal of Veterinary Research*, 40: 1523–6.

Line, S., Morgan, K., Markowitz, H., and Strong, S. (1990) 'Increased cage size does not alter heart rate or behaviour in female rhesus monkeys', *American Journal of Primatology*, 20: 107–13.

Line, S., Markowitz, H., Morgan, K., and Strong, S. (1991) 'Effect of cage size and environmental enrichment on behavioural and physiological responses of rhesus macaques to the stress of daily events', in M. Novak and A. Petto (eds), *Through a Looking Glass: Issues in Psychological Well-Being in Captive Nonhuman Primates*, Washington, DC: American Psychology Association, pp. 160–79.

Linke, S. and Winter, C. (2011) 'Conservation, education or entertainment: what really matters to zoo visitors?', in W. Frost (ed.) *Zoos and Tourism: Conservation, Education, Entertainment?* Bristol: Channel View Publications, pp. 69–81.

Lintzenich, B. A. and Ward, A. M. (1997) 'Hay and pellet ratios: considerations in feeding ungulates', Fact Sheet 006, *AZA Nutrition Advisory Group Handbook*, available online at **http://www.nagonline.net**.

Little, K. A. and Sommer, V. (2002) 'Change of enclosure in langur monkeys: implications for the evaluation of environmental enrichment', *Zoo Biology*, 21: 549–59.

Liu, J. Chen, Y., Guo, L., *et al.* (2006) 'Stereotypic behavior and fecal cortisol level in captive giant pandas in relation to environmental enrichment', *Zoo Biology*, 25: 445–59.

Loeske, E. B., Kruuk, L. E. B., Clutton-Brock, T. H., Albon, S. D., Pemberton, J. M., and Guinness, F. E. (1999) 'Population density affects sex ratio variation in red deer', *Nature*, 399: 460–1.

Lombardi, J. (1998) *Comparative Vertebrate Reproduction*, London: Kluwer.

Lonsdorf, E. V., Ross, S. R., Linick, S. A., Milstein, M. S., and Melber, T. N. (2009) 'An experimental, comparative investigation of tool use in chimpanzees and gorillas', *Animal Behaviour*, 77: 1119–26.

Loskutoff, N. M. (2003) 'Role of embryo technologies in genetic management and conservation of wildlife', in W. Holt, A. Pickard, J. Rodger, and D. Wildt (eds), *Reproductive Science and Integrated Conservation*, Cambridge: Cambridge University Press, pp. 183–94.

Lovell, T. (1998) *Nutrition and Feeding of Fish*, London: Kluwer.

Lozano, G. A. (1998) 'Parasitic stress and self-medication in wild animals', in A. P. Møller, M. Milinski, and P. J. B. Slater (eds), *Advances in the Study of Behavior*. Vol. 27: *Stress and Behavior*, San Diego, CA: Academic Press, pp. 291–317.

Lucentini, L., Caporali, S., Palomba, A., Lancioni, H., and Panara, F. (2006) 'A comparison of conservative DNA extraction methods from fins and scales of freshwater fish: a useful tool for conservation genetics', *Conservation Genetics*, 7: 1009–12.

Ludes, E. and Anderson, J. (1996) 'Comparison of the behaviour of captive white-faced capuchin monkeys (*Cebus capucinus*) in the presence of four kinds of deep litter', *Applied Animal Behaviour Science*, 49: 293–303.

Ludes-Fraulob, E. and Anderson, J. R. (1999) 'Behaviour and preferences among deep litters in captive capuchin monkeys (*Cebus capucinus*)', *Animal Welfare*, 8: 127–34.

Luebke, J. F. and Grajal, A. (2011) 'Assessing mission-related learning outcomes at zoos and aquaria: prevalence, barriers and needs. *Visitor Studies*, 14: 195–208.

Lukas, K. E. (1999) 'A review of nutritional and motivational factors contributing to the performance of regurgitation and reingestion in captive lowland gorillas (*Gorilla gorilla gorilla*)', *Applied Animal Behaviour Science*, 63: 237–49.

Lukas, K. E., Marr, M. J., and Maple, T. L. (1998) 'Teaching operant conditioning at the zoo', *Teaching of Psychology*, 25: 112–16.

Lukas, K. E., Hoff, M. P., and Maple, T. L. (2003) 'Gorilla behavior in response to systematic alternation between zoo enclosures', *Applied Animal Behaviour Science*, 81: 367–86.

Luttrell, L., Acker, L., Urben, M., and Reinhardt, V. (1994) 'Training a large troop of rhesus macaques to co-operate during catching: analysis of the time investment', *Animal Welfare*, 3: 135–40.

Lutz, C. K. and Novak, M. A. (1995) 'Use of foraging racks and shavings as enrichment tools for groups of rhesus monkeys (*Macaca mulatta*)', *Zoo Biology*, 14: 463–74.

Lyles, A. M. and May, R. M. (1987) 'Problems in leaving the ark', *Nature*, 326: 245–6.

Lyons, J., Young, R. J., and Deag, J. M. (1997) 'The effects of physical characteristics of the environment and feeding regime on the behavior of captive felids', *Zoo Biology*, 16: 71–83.

M

McCallum, H. and Jones, M. (2006) 'To lose both would look like carelessness: Tasmanian devil facial tumour disease', *PLoS One*, 4: e342.

McCann, C. M. and Rothman, J. M. (1999) 'Changes in nearest-neighbor associations in a captive group of western lowland gorillas after the introduction of five hand-reared infants', *Zoo Biology*, 18: 261–78.

McCann, C., Buchanan-Smith, H. M., Jones-Engel, L., et al. (2007) *IPS International Guidelines for the Acquisition, Care and Breeding of Non-Human Primates* (2nd edn), available online at **http://www.internationalprimatologicalsociety.org**.

McCarthy, S. (2005) *Becoming a Tiger: How Baby Animals Learn to Live in the Wild*, New York: Harper Perennial.

McCormick, A. E. (1983) 'Canine distemper in African cape hunting dogs (*Lycaon pictus*): possibly vaccine-induced', *Journal of Zoo Animal Medicine*, 14: 66–71.

McCormick, W., Melfi, V., and Muller, C. (2006) 'Lemurs pumping iron', in T. P. Meehan and M. E. Allen (eds), *Proceedings of the Fourth European Zoo Nutrition Conference*, Amsterdam: EAZA Executive Office, p. 42.

Macdonald, C. and Whiten, A. (2011) 'The "Living Links to Human Evolution"' Research Centre in Edinburgh Zoo: a new endeavour in collaboration. *International Zoo Yearbook*, 45: 7–17.

Macdonald, D. (1996) 'Social behaviour of captive bush dogs (*Speothos venaticus*)', *Journal of Zoology*, 239: 525–43.

Macdonald, D. (2001) *The New Encyclopedia of Mammals*, Oxford: Oxford University Press.

Macdonald, D. (2009) *The New Encyclopedia of Mammals* (2nd edn), Oxford: Oxford University Press.

McDonald, P., Greenhalgh, J. F. D., Morgan, C. A., Edwards, R., Sinclair, L., and Wilkinson, R. (2011) *Animal Nutrition* (7th edn), Harlow, Essex: Benjamin Cummings.

McDougall, P. T., Réale, D., Sol, D., and Reader, S. M. (2006) 'Wildlife conservation and animal temperament: causes and consequences of evolutionary change for captive, reintroduced and wild populations', *Animal Conservation*, 9: 39–48.

McDowell, L. R. (2000) *Vitamins in Animal Nutrition: Comparative Aspects to Human Nutrition* (2nd edn), San Diego, CA: Academic Press.

McDowell, L. R. (2003) *Minerals in Animal and Human Nutrition* (2nd edn), San Diego, CA: Academic Press.

McFarland, D. (1999) *Animal Behaviour: Psychobiology, Ethology and Evolution* (3rd edn), Harlow, Essex: Longman.

McGrew, W. C., Brennan, J. A., and Russel, J. (1986) 'An artificial gum-tree for marmosets (*Callithrix jacchus*)', *Zoo Biology*, 5: 45–50.

McKay, S. (2003) 'Personality profiles of the cheetah in the UK and Ireland, in relation to environmental factors and performance variables', in T. C. Gilbert (ed.) *Proceedings of the Fifth Annual Symposium on Zoo Research*, London: BIAZA, pp. 177–89.

McKenna, V., Travers, W., and Wray, J. (eds) (1987) *Beyond the Bars: The Zoo Dilemma*, Wellingborough: Thorsons Publishing Group.

McKenzie, S., Chamove, S., and Feistner, A. (1986) 'Floor-coverings and hanging screens alter arboreal monkey behaviour', *Zoo Biology*, 5: 339–48.

McKinley, J., Buchanan-Smith, H. M., Bassett, L., and Morris, K. (2003) 'Training common marmosets (*Callithrix jacchus*) to cooperate during routine laboratory procedures: ease of training and time investment', *Journal of Applied Animal Welfare Science*, 6: 209–20.

McPhee, M. (2002) 'Intact carcasses as enrichment for large felids: effects on on- and off-exhibit behaviours', *Zoo Biology*, 21: 37–47.

McPhee, M. E. and Carlstead, K. (2010) 'The importance of maintaining natural behaviors in captive mammals', in D. G. Kleiman, K. V. Thompson, and C. Kirk Baer (eds), *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: University of Chicago Press, pp. 303–13.

McPhee, M., Foster, J., Sevenich, M., and Saunders, C. (1998) 'Public perceptions of behavioral enrichment: assumptions gone awry', *Zoo Biology*, 17: 525–34.

McWilliams, D. A. (2005a) 'Nutrition research on calcium homeostasis. I: Lizards (with recommendations)', *International Zoo Yearbook*, 39: 77–84.

McWilliams, D. A. (2005b) 'Nutrition research on calcium homeostasis. II: Freshwater turtles (with recommendations)', *International Zoo Yearbook*, 39: 85–98.

Mace, G. M. (1986) 'Genetic management of small populations', *International Zoo Yearbook*, 24/25: 167–74.

Mace, G. M. (2004) 'The role of taxonomy in species conservation', *Philosophical Transactions of the Royal Society B*, 359: 711–19.

Mace, G. M., Balmford, A., Leader-Williams, N., et al. (2007) 'Measuring conservation success: assessing zoos' contribution', in A. Zimmerman, M. Hatchwell, L. Dickie, and C. West (eds), *Zoos in the 21st Century: Catalysts for Conservation?*, Cambridge: Cambridge University Press, pp. 322–42.

Macri, A. and Patterson-Kane, E. (2011) 'Behavioural analysis of solitary versus socially housed snow leopard (*Panthera uncia*), with the provision of simulated social contact', *Applied Animal Behavioural Science*, 130: 115–23.

Maestripieri, D. (2000) 'Measuring temperament in rhesus macaques: consistency and change in emotionality over time', *Behavioural Processes*, 49: 167–71.

Maestripieri, D. (2001) 'Is there mother–infant bonding in primates?', *Developmental Review*, 21: 93–120.

Maestripieri, D., Schino, G., Aureli, F., and Troisi, A. (1992) 'A modest proposal: displacement activities as an indicator of emotion in primates', *Animal Behaviour*, 44: 967–79.

MAFF (Ministry of Agriculture, Fisheries and Food) (1986) *Manual of Veterinary Parasitological Laboratory Techniques*, Technical Bulletin 18, London: Her Majesty's Stationery Office.

Magin, C., Johnson, T., Groombridge, B., Jenkins, M., and Smith, H. (1994) 'Species extinction, endangerment and captive breeding', in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner (eds), *Creative Conservation: Interactive Management of Wild and Captive Animals*, London: Chapman & Hall, pp. 3–31.

Mairéad, A., Farrell, E. B., and Marples, N. (2000) 'Breeding behavior in a flock of Chilean flamingos (*Phoenicopterus chilensis*) at Dublin Zoo', *Zoo Biology*, 19: 227–37.

Mallapur, A. and Chelan, R. (2002) 'Environmental influences on stereotypy and the activity budget of Indian leopards (*Panthera pardus*) in four zoos in southern India', *Zoo Biology*, 21: 585–95.

Mallapur, A. and Choudhury, B. C. (2003) 'Behavioural abnormalities in captive non-human primates', *Journal of Applied Animal Welfare Science*, 6: 275–84.

Mallapur, A., Qureshi, Q., and Chellam, R. (2002) 'Enclosure design and space utilization by Indian leopards (*Panthera pardus*) in four zoos in southern India', *Journal of Applied Animal Welfare Science*, 5: 111–24.

Mallapur, A., Sinha, A., and Waran, N. (2005) 'Influence of visitor presence on the behaviour of captive lion-tailed macaques (*Macaca silenus*) housed in Indian zoos', *Applied Animal Behaviour Science*, 94: 341–52.

Mallapur, A., Sinha, A., and Waran, N. (2007) 'A world survey of husbandry practices for lion-tailed macaques *Macaca silenus* in captivity', *International Zoo Yearbook*, 41: 166–75.

Mallapur, A., Waran, N. and Sinha, A. (2008) 'The captive audience: the educative influence of zoos on their visitors in India', *International Zoo Yearbook*, 42: 214–24.

Mallet, J. (2001) 'Mimicry: an interface between psychology and evolution', *Proceedings of the National Academy of Sciences of the USA*, 98: 8928–30.

Mallinson, J. (1995) 'Zoo breeding programmes: balancing conservation and animal welfare', *Dodo: Journal of the Jersey Wildlife Preservation Trust*, 3110: 66–73.

Malmkvist, J. and Hansen, S. W. (2001) 'The welfare of farmed mink (*Mustela vison*) in relation to behavioural selection: a review', *Animal Welfare*, 10: 41–52.

Maloney, M. A., Leighty, K. A., Kuhar, C. W., and Bettinger, T. L. (2011) 'Behavioral responses of silverback gorillas (*Gorilla gorilla gorilla*) to videos', *Journal of Applied Animal Welfare Science*, 14: 96–108.

Manly, B. F. J. (1998) *Randomization, Bootstrap and Monte Carlo Methods in Biology* (2nd edn), London: Chapman & Hall.

Mann, J. R. (1988) 'Full-term development of mouse eggs fertilized by a spermatozoan microinjected under the zona pellucida', *Biology of Reproduction*, 38: 1077–83.

Manning, A. and Dawkins, M. S. (2012) *An Introduction to Animal Behaviour* (6th edn), Cambridge: Cambridge University Press.

Maple, T. L. and Bashaw, M. J. (2010). Research trends in zoos. In D. G. Kleiman, K. V. Thompson, and C. Kirk Baer (editors). *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: University of Chicago Press, pp. 288–98.

Maple, T. and Finlay, T. (1989) 'Applied primatology in the modern zoo', *Zoo Biology (Supplement)*, 112: 101–16.

Marcellini, D. L. and Jenssen, T. A. (1988) 'Visitor behavior in the National Zoo's reptile house', *Zoo Biology*, 7: 329–38.

Margulis, S. W. and Westhus, E. J. (2008) 'Evaluation of different observational sampling regimes for use in zoological parks', *Applied Animal Behaviour Science*, 110: 363–76.

Margulis, S. W., Hoyos, C., and Anderson, M. (2003) 'Effect of felid activity on zoo visitor interest', *Zoo Biology*, 22: 587–99.

Maria, G. A. (2006) 'Public perception of farm animal welfare in Spain', *Livestock Science*, 103: 250–6.

Marino, L., Lilienfeld, S. O., Malamud, R., Nobis, N., and Broglio, R. (2010) 'Do zoos and aquariums promote attitude change in visitors? A critical evaluation of the American zoo and aquarium study', *Society and Animals*, 18: 126–38.

Marker-Kraus, L. (1997) 'History of the cheetah: *Acinonyx jubatus* in zoos 1829–1994', *International Zoo Yearbook*, 35: 27–43.

Marker-Kraus, L. and Grisham, J. (1993) 'Captive breeding of cheetahs in North American Zoos: 1987–1991', *Zoo Biology*, 12: 5–18.

Markowitz, H. (1982) *Behavioural Enrichment in the Zoo*, New York: Van Nostrand Reinhold.

Markowitz, H. and Woodworth, G. (1978) 'Experimental analysis and control of group behaviour', in H. Markowitz and V. J. Stevens (eds), *Behavior of Captive Wild Animals*, Chicago, IL: Nelson-Hall, pp. 107–31.

Markowitz, H., Schmidt, M., and Moody, A. (1978) 'Behavioural engineering and animal health in the zoo', *International Zoo Yearbook*, 18: 190–5.

Markowitz, H., Aday, C., and Gavazzi, A. (1995) 'Effectiveness of acoustic prey: environmental enrichment for a captive African leopard (*Panthera pardus*)', *Zoo Biology*, 14: 371–9.

Markwell, K. and Cushing, N. (2009) 'The serpent's stare meets the tourist's gaze: strategies of display at the Australian Reptile Park', *Current Issues in Tourism*, 12: 475–88.

Maroldo, G. K. (1978) 'Zoos worldwide as settings for psychological research', *American Psychologist*, 33: 1000–4.

Marqués, H., Navidad, G., Baucells, M., and Albanell, E. (2001) 'Animals' nutritional wisdom: pros and cons of cafeteria-style feeding', *Zoo Nutrition News (EAZA)*, 2: 23–5.

Marriner, L. M. and Drickamer, L. C. (1994) 'Factors influencing stereotyped behaviour of primates in a zoo', *Zoo Biology*, 13: 267–75.

Marris, E. (2007) 'Linnaeus at 300: the species and the specious', *Nature*, 446: 250–3.

Martel, Y. (2002) *Life of Pi*, Edinburgh: Canongate.

Martin, J. E. (2002) 'Early life experiences: activity levels and abnormal behaviours in resocialised chimpanzees', *Animal Welfare*, 11: 419–36.

Martin, J. E. (2005) 'The effects of rearing conditions on grooming and play behaviour in captive chimpanzees', *Animal Welfare*, 14: 125–33.

Martin, P. and Bateson, P. (2007) *Measuring Behaviour: An Introductory Guide* (3rd edn), Cambridge: Cambridge University Press.

Martin, R and Melfi, V. A. (2013) 'A comparison of zoo animal behaviour in the presence of familiar and unfamiliar people', *Applied Animal Behaviour Science,* submitted for publication.

Masefield, W. (1999) 'Forage preferences and enrichment in a group of captive Livingstone's fruit bats *Pteropus livingstonii*', *Dodo. Journal of the Jersey Wildlife Preservation Trust*, 35: 48–56.

Maser, J. and Gallup, G. J. (1974) 'Tonic immobility in the chicken: catalepsy potentiation by uncontrollable shock and alleviation by imipramine', *Psychosomatic Medicine*, 36: 199–205.

Mason, G. J. (1991) 'Stereotypies: a critical review', *Animal Behaviour*, 41: 1015–37.

Mason, G. J. (2006) 'Stereotypic behaviour in captive animals: fundamentals, and implications for welfare and beyond', in G. J. Mason (ed.), *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*, Wallingford, Oxon: CABI Publishing, pp. 325–56.

Mason, G. J. (2010) 'Species differences in responses to captivity: stress, welfare and the comparative method', *Trends in Ecology and Evolution*, 25: 713–21.

Mason, G. (2011) 'Invertebrates welfare: where is the real evidence for conscious affective states? ', *Trends in Ecology and Evolution,* 26: 212–13.

Mason, G. J. and Latham, N. R. (2004) 'Can't stop, won't stop: is stereotypy a reliable animal welfare indicator?', *Animal Welfare*, 13: 557–69.

Mason, G. J. and Littin, K. E. (2003) 'The humaneness of rodent pest control', *Animal Welfare*, 12: 1–37.

Mason, G. J. and Rushen, J. (eds) (2006) *Stereotypic Animal Behaviour: Fundamentals and Applications to Welfare*, Wallingford, Oxon: CABI Publishing.

Mason, G. J., Cooper, J., and Clarebrough, C. (2001) 'Frustrations of fur-farmed mink', *Nature*, 410: 35–6.

Mason, G., Clubb, R., Latham, N., and Vickery, S. (2007) 'Why and how should we use environmental enrichment to tackle stereotypic behaviour?' *Applied Animal Behaviour Science* 102: 163–88.

Mason, P. (2000) 'Zoo tourism: the need for more research', *Journal of Sustainable Tourism*, 8: 333–9.

Mason, P. (2008) 'Roles of the modern zoo: conflicting or complementary?', *Tourism Review International*, 11: 251–63.

Mather, J. (1992) 'Underestimating the octopus', in H. Davis and D. Balfour (eds), *The Inevitable Bond: Examining Scientist–Animal Interactions*, Cambridge: Cambridge University Press, pp. 240–9.

Mathews, F., Orrors, M., McLaren, G., Gelling, M., and Foster, R. (2005) 'Keeping fit on the ark: assessing

the suitability of captive-bred animals for release', *Biological Conservation*, 121: 569–77.

Matthews, K. (1998) *Behavioural Studies of Sulawesi Crested Black Macaques (*Macaca nigra*): Managing Males in Captivity*, Trinity, Jersey: Durrell Wildlife Conservation Trust.

May, R. M. (2011) 'Why should we be concerned about loss of biodiversity', *Comptes Rendues Biologies*, 334: 346–350.

May, R. M. and Lyles, A. M. (1987) 'Living Latin binomials', *Nature*, 326: 642–3.

Mayor, J. (1984) 'Hand-feeding an orphaned scimitar-horned oryx *Oryx dammah* calf after its integration with the herd', *International Zoo Yearbook*, 23: 243–8.

Mayr, E. (1942) *Systematics and the Origin of Species*, New York: Columbia University Press.

Mazur, N. A. (2001) *After the Ark? Environmental Policy Making and the Zoo*, Melbourne: Melbourne University Press.

Meagher, R. K., and Mason, G. J. (2012) 'Environmental enrichment reduces signs of boredom in caged mink', *PLoS One* 7:11, e49180.

Measey, G., Gower, D., Oommen, O., and Wilkinson, M. (2001) 'Permanent marking of a fossorial caecilian, *Gegeneophis ramaswamii* (Amphibia: Gymnophiona: Caeciliidae)', *Journal of South Asian Natural History*, 5: 141–7.

Meehan, C. L. and Mench, J. A. (2002) 'Environmental enrichment affects the fear and exploratory responses to novelty of young Amazon parrots', *Applied Animal Behaviour Science*, 79: 75–88.

Meehan, C. L. and Mench, J. A. (2007) 'The challenge of challenge: can problem solving opportunities enhance animal welfare?', *Applied Animal Behaviour Science*, 102: 246–61.

Meehan, C. L., Garner, J. P., and Mench, J. A. (2003) 'Isosexual pair housing improves the welfare of young Amazon parrots', *Applied Animal Behaviour Science*, 81: 73–88.

Meehan, C. L., Garner, J. P., and Mench, J. A. (2004) 'Environmental enrichment and development of cage stereotypy in orange-winged Amazon parrots (*Amazona amazonica*)', *Developmental Psychobiology*, 44: 209–16.

Meehan, T. P. (2012) 'AAZV guidelines for zoo and aquarium veterinary medical programs and veterinary hospitals', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 125–8.

Melfi, V. A. (2001) 'Identification and evaluation of the captive environmental factors that affect the behaviour of Sulawesi crested black macaques (*Macaca nigra*)', unpublished PhD thesis, Department of Zoology, University of Dublin, Trinity College Dublin, Ireland.

Melfi, V. A. (2005) 'The appliance of science to zoo-housed primates', *Applied Animal Behaviour Science*, 90: 97–106.

Melfi, V. A. (2009) 'There are big gaps in our knowledge, and thus approach, to zoo animal welfare: a case for evidence-based zoo animal management', *Zoo Biology*, 28: 574–88.

Melfi, V. (2010) 'Selamatkan Yaki! Conservation of Sulawesi crested black macaques *Macaca nigra*', in Gursky-Doyen, S. and Supriatna, J. (eds), *Indonesian Primates*, New York: Springer, pp. 343–57.

Melfi, V. A. (2012a) 'Gibbons: probably the most endangered primates in the world', *International Zoo Yearbook*, 46: 239–40.

Melfi, V. A. (2012b) '*Ex situ* gibbon conservation: status, management and birth sex ratios', *International Zoo Yearbook*, 46: 241–51.

Melfi, V. A. (2013) 'Is training enriching', *Applied Animal Behaviour Science*, in press.

Melfi, V. A. and Feistner, A. T. C. (2002) 'A comparison of the activity budgets of wild and captive Sulawesi crested black macaques (*Macaca nigra*)', *Animal Welfare*, 11: 213–22.

Melfi, V. and Hosey, G. (2011) 'Capacity building for better animal welfare', *International Zoo Yearbook*, 45: 274–81.

Melfi, V. A. and Hosey, G. R. (2012) *Zoo Research Guidelines: Multi-zoo Studies*. London: BIAZA.

Melfi, V. and Knight, K. (2009) 'Public perceptions of carnivore feeding methods: preliminary results from an international study', in A. Hartley and S. K. Forbes(eds), *Proceedings of the 9th Annual Symposium on Zoo Research*, London: BIAZA, p. 19.

Melfi, V. and Poyser, F. (2007) '*Trichuris* burdens in zoo-housed *Colobus guereza*', *International Journal of Primatology*, 28: 1449–56.

Melfi, V. A. and Thomas, S. (2005) 'Can training zoo-housed primates compromise their conservation? A case study using Abyssinian colobus monkeys (*Colobus guereza*)', *Anthrozoös*, 18: 304–17.

Melfi, V. A., Garcia, L., Dicks, J., *et al.* (2004a) 'Wire hay racks: simple but effective enrichment', data presented at the BIAZA Elephant TAG meeting, Chester Zoo.

Melfi, V. A., McCormick, W., and Gibbs, A. (2004b) 'A preliminary assessment of how zoo visitors evaluate animal welfare according to enclosure style and the expression of behaviour', *Anthrozoös*, 17: 98–108.

Melfi, V. A., Bowkett, A., Plowman, A. B., and Pullen, K. (2007) 'Do zoo designers know enough about animals?', in A. B. Plowman and S. Tonge (eds), *Innovation or Replication: Proceedings of the Sixth International Symposium on Zoo Design*, Paignton, Devon: Whitley Wildlife Conservation Trust, pp. 119–27.

Mellen, J. D. (1991) 'Factors influencing reproductive success in small captive exotic felids (*Felis* spp.): a multiple regression analysis', *Zoo Biology*, 10: 95–110.

Mellen, J. D. (1992) 'Effects of early rearing experience on subsequent adult sexual behavior using domestic cats (*Felis catus*) as a model for exotic small felids', *Zoo Biology*, 11: 17–32.

Mellen, J. D. (1994) 'Survey and interzoo studies used to address husbandry problems in some zoo vertebrates', *Zoo Biology*, 13: 459–70.

Mellen, J. D. and Ellis, S. (1996) 'Animal learning and husbandry training techniques', in D. G. Kleiman, M. E. Allen, K. V. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago Press, pp. 88–99.

Mellen, J. D. and MacPhee, M. S. (2001) 'Philosophy of environmental enrichment: past, present, and future', *Zoo Biology*, 20: 211–26.

Mellen, J. and MacPhee, M. (2010) 'Animal learning and husbandry training for management', in D. G. Kleiman, K. V. Thompson, and C. Kirk Baer (eds), *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: University of Chicago Press, pp. 314–28.

Meller, C. L., Croney, C. C., and Shepherdson, D. (2007) 'Effects of rubberized flooring on Asian elephant behavior in captivity', *Zoo Biology*, 26: 51–61.

Mello, I., Nordensten, L., and Amundin, M. (2005) 'Reactions of three bottlenose dolphin dams with calves to other members of the group in connection with nursing', *Zoo Biology*, 24: 543–55.

Melnick, D. and Pearl, M. (1987) 'Cercopithecines in multimale groups: genetic diversity and population structure', in B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker (eds), *Primate Societies*, Chicago, IL: Chicago University Press, pp. 121–34.

Menargues, A., Urios, V, and Mauri (2008) 'Welfare assessment of captive Asian elephants (*Elephas maximus*) and Indian rhinoceros (*Rhinoceros unicornis*) using salivary cortisol measurement', *Animal Welfare*, 17, 305–12

Mench, J. A. (1998) 'Thirty years after Brambell: whither animal welfare science?', *Journal of Applied Animal Welfare Science*, 1: 91–102.

Mendelson, J. R., III, Lips, R., Gagliardo, R. W., et al. (2006) Confronting amphibian declines and extinctions. *Science, NY*, 313: 48.

Mendl, M., Burman, O. H. P., Parker, R. M. A., and Paul, E. S. (2009) 'Cognitive bias as an indicator of animal emotion and welfare: emerging evidence and underlying mechanisms', *Applied Animal Behaviour Science*, 118: 161–81.

Mensink, M. and Shafternaar, W. (1998) 'When bad things happen to bats: the occurrence of a *Lyssavirus* in a closed population of Egyptian frugivorous bats (*Rousettus aegyptiacus*) at Rotterdam Zoo', *Proceedings of the Annual Meeting of the European Association of Zoo and Wildlife Veterinarians*, Liebefeld-Berne, Switzerland: EAZWV, pp. 147–51.

Menzel, C. (1991) 'Cognitive aspects of foraging in Japanese monkeys', *Animal Behaviour*, 41: 397–402.

Meretsky, V. J., Snyder, N. F. R., Beissinger, F. R., Clendenen, D. A., and Wiley, J. W. (2000) 'Demography of the Californian condor: implications for reestablishment', *Conservation Biology*, 14: 957–67.

Mete, A., Hendriks, H. G., Klaren, P. H. M., et al. (2003) 'Iron metabolism in mynah birds (*Gracula religiosa*) resembles human hereditary haemochromatosis', *Avian Pathology*, 32: 625–32.

Meyer-Holzapfel, M. (1968) 'Abnormal behaviour in zoo animals', in M. W. Fox (ed.), *Abnormal Behavior in Animals*, Philadelphia, PA: W. B. Saunders, pp. 476–503.

Midgley, M. (1983) *Animals and Why They Matter*, Athens, GA: University of Georgia Press.

Mikota, S. K. (2007) 'Tuberculosis in elephants', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (6th edn), St Louis, MO: Saunders Elsevier, pp. 355–64.

Mikota, S. K., Larsen, R. S., and Montali, R. J. (2000) 'Tuberculosis in elephants in North America', *Zoo Biology*, 19: 393–403.

Millam, J. R., Kenton, B., Jochim, L., Brownback, T., and Brice, A. T. (1995) 'Breeding orange-winged Amazon parrots in captivity', *Zoo Biology*, 14: 275–84.

Millar, J. S. and Hickling, G. J. (1990) 'Fasting endurance and the evolution of mammalian body size', *Functional Ecology*, 4: 5–12.

Miller, A., Leighty, K. A., Maloney, M. A., Kuhar, C. W., and Bettinger, T. L. (2011) 'How access to exhibit space impacts the behavior of female tigers (*Panthera tigris*)', *Zoo Biology* 30: 479–86.

Miller, B., Conway, W., Reading, R. P., *et al.* (2004) 'Evaluating the conservation mission of zoos, aquariums, botanical gardens and natural history museums', *Conservation Biology*, 18: 86–93.

Miller, H. (2006) 'Cloacal and buccal swabs are a reliable source of DNA for microsatellite genotyping of reptiles', *Conservation Genetics*, 7: 1001–3.

Miller, L. (2012) 'Visitor reaction to pacing behavior: influence on the perception of animal care and interest in supporting zoological institutions', *Zoo Biology*, 31: 242–8.

Miller, L. J., Kuczaj, S. and Herzing, D. (2011a) 'Stereotypic behavior in wild marine carnivores?', *Zoo Biology* 30: 365–70.

Miller, L. J., Mellen, J., Greer, T., and Kuczaj II, S. A. (2011b) 'The effects of education programmes on Atlantic bottlenose dolphin (*Tursiops truncatus*) behaviour', *Animal Welfare*, 20: 159–72.

Miller, L. J., Zeigler-Hill, V., Mellen, J., Koeppel, J., Greer, T., and Kuczaj, S. (2013) Dolphin shows and interaction programs: benefits for conservation education? *Zoo Biology*, 32: 45–53.

Millman, S. T. and Duncan, I. J. H. (2000) 'Strain differences in aggressiveness of male domestic fowl in response to a male model', *Applied Animal Behaviour Science*, 66: 217–33.

Millman, S. T., Duncan, I. J. H., Stauffacher, M., and Stookey, J. M. (2004) 'The impact of applied ethologists and the International Society for Applied Ethology in improving animal welfare', *Applied Animal Behaviour Science*, 86: 299–311.

Millspaugh, J. J. and Washburn, B. E. (2003) 'Within-sample variation of fecal glucocorticoid measurements', *General and Comparative Endocrinology*, 132: 21–6.

Millspaugh, J. J. and Washburn, B. E. (2004) 'Use of fecal glucocorticoid metabolite measures in conservation biology research: considerations for application and interpretation', *General and Comparative Endocrinology*, 138: 189–99.

Misslin, R. and Cigrang, M. (1986) 'Does neophobia necessarily imply fear or anxiety?', *Behavioral Proceedings*, 12: 45–50.

Mistlberger, R. E. (1994) 'Circadian food-anticipatory activity: formal models and physiological mechanisms', *Neuroscience and Biobehavioral Reviews*, 18: 171–95.

Mitchell, G. and Gomber, J. (1976) 'Moving laboratory rhesus monkeys (*Macaca mulatta*) to unfamiliar home cages', *Primates*, 17: 543–7.

Mitchell, G., Herring, F., Obradovich, S., *et al.* (1991a) 'Effects of visitors and cage changes on the behaviours of mangabeys', *Zoo Biology*, 10: 417–23.

Mitchell, G., Obradovich, S. D., Herring, F. H., Dowd, B., and Tromborg, C. (1991b) 'Threats to observers, keepers, visitors, and others by zoo mangabeys (*Cercocebus galeritus chrysogaster*)', *Primates*, 32: 515–22.

Mitchell, G., Herring, F., and Obradovich, S. (1992a) 'Like threaten like in mangabeys and people', *Anthrozoös*, 5: 106–12.

Mitchell, G., Tromborg, C. T., Kaufman, J., Bargabus, S., Simoni, R., and Geissler, V. (1992b) 'More on the "influence" of zoo visitors on the behaviour of captive primates', *Applied Animal Behaviour Science*, 35: 189–98.

Mitchell, G., van Schalkwyk, O. L., and Skinner, J. D. (2006). The calcium and phosphorus content of giraffe *Giraffa camelopardalis* and buffalo *Syncerus caffer* skeletons. *Journal of Zoology* 267: 55–61.

Mitchell, H. and Hosey, G. (2005) *Zoo Research Guidelines: Studies of the Effects of Human Visitors on Zoo Animal Behaviour*, London: BIAZA.

Mitsui, S., Yamamoto, M., Nagawawa, M., *et al.* (2011) 'Urinary oxytocin as a noninvasive biomarker of positive emotion in dogs', *Hormones and Behaviour*, 60: 239–43.

Moberg, G. P. and Mench, J. A. (eds) (2000) *The Biology of Animal Stress: Basic Principles and Implications for Animal Welfare*, Wallingford, Oxon: CABI Publishing.

Moe, M. (1993) *The Marine Aquarium Reference: Systems and Invertebrates*, Plantation, FL: Green Turtle Publications.

Moehrenschlager, A., Alexander, S., and Brichieri-Colombi, T. (2006) *Habitat Suitability and Population Viability Analysis for Reintroduced Swift Foxes in Canada and Northern Montana*, Report No. 2, Centre for Conservation Research, Calgary, Canada.

Mollá, M. I., Quevedo, M. A., and Castro, F. (2011) 'Bobcat (*lynx rufus*) breeding in captivity: the importance of environmental enrichment', *Journal of Applied Animal Welfare Science*, 14: 85–95.

Molloy, L. and Hart, J. A. (2002) 'Duiker food selection: palatability trials using natural foods in the Ituri Forest, Democratic Republic of Congo', *Zoo Biology*, 21: 149–59.

Molony, V. and Kent, J. E. (1997) 'Assessment of acute pain in farm animals using behavioral and physiological measurements', *Journal of Animal Science*, 75: 266–72.

Montanha, J. C., Silva, S. L., and Boere, V. (2009) 'Comparison of salivary cortisol concentrations in jaguars kept in captivity with differences in exposure to the public', *Ciência Rural*, 39: 1745–51.

Montaudouin, S. and Le Pape, G. (2004) 'Comparison of the behaviour of European brown bears (*Ursus arctos arctos*) in six different parks, with particular attention to stereotypies', *Behavioural Processes*, 67: 235–44.

Montaudouin, S. and Le Pape, G. (2005) Comparison between 28 zoological parks: stereotypic and social behaviours of captive brown bears (*Ursus arctos*)', *Applied Animal Behaviour Science*, 92: 129–41.

Moodie, E. M. and Chamove, A. S. (1990) 'Brief threatening events beneficial for captive tamarins?', *Zoo Biology*, 9: 275–86.

Moore, B. D., Marsh, K. J., Wallis, I. R., and Foley, W. J. (2005) 'Taught by animals: how understanding diet selection leads to better zoo diets', *International Zoo Yearbook*, 39: 43–61.

Moore, T. L., Killiany, R. J., Herndon, J. G., Rosene, D. L., and Moss, M. B. (2006) 'Executive system dysfunction occurs as early as middle-age in the rhesus monkey', *Neurobiology of Aging*, 27: 1484–93.

Moran, G. and Sorensen, L. (1984) 'The behavioural researcher and the zoological park', *Applied Animal Behaviour Science*, 13: 143–55.

Morgan, J. M. and Hodgkinson, M. (1999) 'The motivation and social orientation of visitors attending a contemporary zoological park', *Environment and Behavior*, 31: 227–39.

Morgan, K. N. and Tromborg, C. T. (2007) 'Sources of stress in captivity', *Applied Animal Behaviour Science*, 102: 262–302.

Moritz, C. (1994) 'Defining "evolutionarily significant units" for conservation', *Trends in Ecology and Evolution*, 9: 373–5.

Mormede, P., Andanson, S., Auperin, B., *et al.* (2007) 'Exploration of the hypothalamic–pituitary–adrenal function as a tool to evaluate animal welfare', *Physiology and Behavior*, 92: 317–39.

Morris, C. L. M., Grandin, T., and Irlbeck, N. A. (2011) 'Companion Animals Symposium. Environmental enrichment for companion, exotic, laboratory animals', *Journal of Animal Science*, 89: 4227–38

Morris, D. (1964) 'The response of animals to a restricted environment', *Symposium of the Zoological Society of London*, 13: 99–118.

Morris, D. (1969) *The Human Zoo*, London: Jonathan Cape.

Morton, A. C. (1990) 'Captive breeding of butterflies and moths. II: Conserving genetic variation and managing biodiversity', *International Zoo Yearbook*, 30: 89–97.

Moss, A. and Esson, M. (2010) 'Visitor interest in zoo animals and the implications for collection planning and zoo education programmes', *Zoo Biology*, 29: 715–31.

Moss, A. and Esson, M. (2013) 'The educational claims of zoos: where do we go from here?' *Zoo Biology*, 32: 13–18.

Moss, A., Esson, M., and Bazley, S. (2010) 'Applied research and zoo education: the evolution and evaluation of a public talks program using unobtrusive video recording of visitor behaviour', *Visitor Studies,* 13: 23–40.

Mowles, S. L., Cotton, P. A., and Briffa, M. (2012) 'Consistent crustaceans: the identification of stable behavioural syndromes in hermit crabs', *Behavioral Ecology and Sociobiology*, 66: 1087–94.

Moyle, M. (1989) 'Vitamin D and UV radiation: guidelines for the herpetoculturist', in M. Uricheck (ed.), *Proceedings of the 13th International Herpetological Symposium on Captive Propagation and Husbandry*, Thurmont, MD: Zoological Consortium, pp. 61–70.

Muhic, J., Abbott, E., and Ward, M. (2012) 'The warru (*Petrogale lateralis* MacDonnell Ranges race) reintroduction project on the Anangu Pitjantjatjara Yankunytjatjara Lands, South Australia', *Ecological Management and Restoration*, 13: 89–92.

Murphy, J. B. (2007) *Herpetological History of the Zoo and Aquarium World*, Melbourne, FL: Krieger.

Murray, J., Murray, E., Johnson, M. S., and Clarke, B. (1988) 'The extinction of *Partula* on Moorea', *Pacific Science*, 42: 150–3.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., and Kent, J. (2000) 'Biodiversity hotspots for conservation priorities', *Nature*, 403: 853–58.

Myers, O. E., Saunders, C. D., and Birjulin, A. A. (2004) 'Emotional dimensions of watching zoo animals: an experience sampling study building on insights from psychology', *Curator*, 47: 299–321.

N

Naldo, J. L. and Samour, J. H. (2004) 'Causes of morbidity and mortality in falcons in Saudi Arabia', *Journal of Avian Medicine and Surgery*, 18: 229–41.

Napolitano, F., de Rosa, G., Grasso, F., and Wemelsfelder, F. (2012) 'Qualitative behaviour assessment of dairy buffaloes (*Bubalus bubalis*)', *Applied Animal Behaviour Science*, 141: 91–100.

Narayan, E. J., Cockrem, J. F., and Hero, J. M. (2011) 'Urinary corticosterone metabolite responses to capture and captivity in the cane toad (*Rhinella marina*)', *General and Comparative Endocrinology*, 173: 371–7.

Nash, L. and Chilton, S. (1986) 'Space or novelty? Effects of altered cage size on galago behaviour', *American Journal of Primatology*, 10: 37–50.

Nelson, R. (2000) *An Introduction to Behavioral Endocrinology*, Sunderland, MA: Sinauer Associates.

Neptune, D. and Walz, D. (2005) 'Thinking outside the cardboard box: taking enrichment to the next level', in N. Clum, S. Silver, and P. Thomas (eds), *Seventh Conference on Environmental Enrichment*, San Diego, CA: The Shape of Enrichment, pp. 90–5.

Newberry, R. (1995) 'Environmental enrichment: increasing the biological relevance of captive environments', *Applied Animal Behavioural Science*, 44: 229–43.

Nicholls, H. (2009) 'Ten extinct beasts that could walk the Earth again', *New Scientist*, 201: 24–8.

Nicholls, N. (2003) 'Development of a method to determine behavioural need in Mediterranean tortoise *Testudo hermanni*', *Federation Research Newsletter*, 4: 3.

Nieuwenhuijsen, K. and de Waal, F. (1982) 'Effects of spatial crowding on social behavior in a chimpanzee colony', *Zoo Biology*, 1: 5–28.

Nijboer, J. and Hatt, J. (2000) *Zoo Animal Nutrition*, Vol. I, Fürth, Germany: Filander Verlag.

Noë, R. and Bshary, R. (1997) 'The formation of red colobus–Diana monkey associations under predation pressure from chimpanzees', *Proceedings of the Royal Biological Society*, 264: 253–9.

Nogge, G. (1997) 'Introduction: zoo research—the role of the EAZA Research Committee', *Applied Animal Behaviour Science*, 51: 195–7.

Norcup, S. (2001) *European Endangered Species Programme Studbook for Sulawesi Crested Black Macaques (Macaca nigra)* (4th edn), Trinity, Jersey: Durrell Wildlife Conservation Trust.

Norris, R. (2005) 'Transport of animals by sea', *OIE Scientific and Technical Review*, 24: 673–81.

Norton, B. G., Hutchins, M., Stevens, E., and Maple, T. L. (eds) (1995) *Ethics on the Ark: Zoos, Animal Welfare and Wildlife Conservation*, Washington, DC: Smithsonian Institute Press.

Novak, M. A. (2003) 'Self-injurious behaviour in rhesus monkeys: new insights into its etiology, physiology, and treatment', *American Journal of Primatology*, 59: 3–19.

Novak, M. A., Musante, A., Munroe, H., O'Neill, P. L., Price, C., and Suomi, S. J. (1993) 'Old, socially housed rhesus monkeys manipulate objects', *Zoo Biology*, 12: 285–98.

NRC (National Research Council) (1982) *Nutrient Requirements of Mink and Foxes*, Washington, DC: National Academy Press.

NRC (National Research Council) (2001) *Nutrient Requirements of Dairy Cattle*, Washington, DC: National Academy Press.

NRC (National Research Council) (2006) *Nutrient Requirements of Dogs and Cats*, Washington, DC: National Academy Press.

NRC (National Research Council) (2012) *Nutrient Requirements of Swine*, Washington, DC: National Academy Press.

Nussey, D. H., Froy, H., Lemaitre, J. F., Gaillard, J. M., and Austaud, S. N. (2012) 'Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology', *Ageing Research Reviews*, 12: 214–25.

Nyhus, P. J., Tilson, R. L., and Tomlinson, J. L. (2003) 'Dangerous animals in captivity: *ex situ* tiger conflict and implications for private ownership of exotic animals,' *Zoo Biology*, 22: 573–86.

O

Oaks, J. L., Gilbert, M., Virani, M. Z., *et al*. (2004) 'Diclofenac residues as the cause of vulture population decline in Pakistan', *Nature*, 427: 630–3.

Oates, J. (1989) 'Food distribution and foraging behaviour', in B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Struhsaker (eds), *Primate Societies*, Chicago, IL: Chicago University Press, pp. 197–209.

O'Brien, J. (2006) 'Effects of conspecific playback recordings on a pair of Toco toucans', *The Shape of Enrichment*, 15: 3–5.

O'Brien, S., Roelke, M., Marker, L., *et al.* (1985) 'Genetic basis for species vulnerability in the cheetah', *Science*, 227: 1428–34.

O'Brien, T. and Kinnaird, M. (1997) 'Behaviour, diet and movement of the Sulawesi crested black macaque', *International Journal of Primatology*, 18: 321–51.

O'Connor, K. I. (2000) 'Mealworm dispensers as environmental enrichment for captive Rodrigues fruit bats (*Pteropus rodricensis*)', *Animal Welfare*, 9: 123–37.

O'Donovan, D., Hindle, J. E., McKeown, S., and O'Donovan, S. (1993) 'Effect of visitors on the behaviour of female cheetahs *Acinonyx jubatus*', *International Zoo Yearbook*, 32: 238–44.

Oftedal, O. T. and Allen, M. E. (1996) 'Nutrition and dietary evaluation in zoos', in D. Kleiman, M. E. Allen, K. V. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago Press, pp. 109–16.

Oftedal, O. T., Baer, D. J., and Allen, M. E. (1996) 'The feeding and nutrition of herbivores', in D. Kleiman, M. E. Allen, K. V. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago Press, pp. 129–38.

Ogden, J., Lindburg, D., and Maple, T. (1993) 'Preference for structural environmental features in captive lowland gorillas', *Zoo Biology*, 12: 381–95.

Olney, P. (1975) 'Walk-through avaries', in A. Michelmore (ed.), *Proceedings of the First International Symposium on Zoo Design and Construction*, Paignton, Devon: Whitley Wildlife Conservation Trust, pp. 130–5.

Olney, P. (1980) 'The London Zoo and Whipsnade Zoo', in L. S. Zuckerman (ed.), *Great Zoos of the World: Their Origins and Significance*, London: Weidenfeld & Nicolson, pp. 37–59.

Olney, P. J. S., Mace, G. M., and Feistner, A. T. C. (eds) (1994) *Creative Conservation: Interactive Management of Wild and Captive Animals*, London: Chapman & Hall.

O'Regan, H. J. (2001) 'Morphological effects of captivity in big cat skulls', in S. Wehnelt and C. Hudson (eds), *Proceedings of the Third Annual Symposium on Zoo Research*, London: BIAZA, pp. 18–22.

O'Regan, H. J. and Kitchener, A. C. (2005) 'The effects of captivity on the morphology of captive, domesticated and feral mammals', *Mammal Review*, 35: 215–30.

Ortega, J., Franco, R., Adams, B. A., Ralls, K., and Maldonado, J. E. (2004) 'A reliable, non-invasive method for sex determination in the endangered San Joaquin kit fox (*Vulpes macrotis mutica*) and other canids', *Conservation Genetics*, 5: 715–18.

Osawa, R., Blanchard, W. H., and O'Callaghan, P. G. (1993) 'Microbiological studies of the intestinal microflora of the koala, *Phascolarctos cinereus*', *Australian Journal of Zoology*, 41: 611–20.

Ostrowski, S., Bedin, E., Lenain, D. M., and Abuzinada, A. H. (1998) 'Ten years of Arabian oryx conservation breeding in Saudi Arabia: achievements and regional perspectives', *Oryx*, 32: 209–22.

Ott-Joslin, J. E. (1993) 'Zoonotic diseases of nonhuman primates', in M. E. Fowler (ed.), *Zoo and Wild Animal Medicine: Current Therapy* (3rd edn), Philadelphia, PA: W. B. Saunders, pp. 358–73.

Overmier, J. B., Patterson, J., and Wielkiewics, R. M. (1980) 'Environmental contingencies as sources of stress in animals', in S. Levine and H. Ursin (eds) *Coping and Health*, New York: Plenum Press, pp. 1–38.

Owen, M. A., Swaisgood, R. R., Czekala, N. M., Steinman, K., and Lindburg, D. G. (2004) 'Monitoring stress in captive giant pandas (*Ailuropoda melanoleuca*): behavioural and hormonal responses to ambient noise', *Zoo Biology*, 23: 147–64.

Owen, M. A., Swaisgood, R. R., Czekala, N. M., and Lindburg, D. G. (2005) 'Enclosure choice and well-being in giant pandas: is it all about control?', *Zoo Biology*, 24: 475–81.

P

Packard, J., Babbitt, K., Hannon, P., and Grant, W. (1990) 'Infanticide in captive collared peccaries (*Tayassu tajacu*)', *Zoo Biology*, 9: 49–53.

Pankhurst, S. J. (1998) 'The social organisation of the mara (*Dolichotis patagonum*) at Whipsnade Wild Animal Park', unpublished PhD thesis, University of Cambridge.

Pankhurst, S. J. and Knight, K. (2008) *Zoo Research Guidelines: Behavioural Profiling of Zoo Animals*, London: BIAZA.

Pankhurst, S. J., Plumb, A., and Walter, O. (2008) *Zoo Research Guidelines: Getting Zoo Research Published*, London: BIAZA.

Pankhurst, S. J., Knight, K., Walter, O., and Waters, S. S. (eds) (2009) *Zoo Research Guidelines: Behavioural Profiling*. London: BIAZA.

Panksepp, J. (2011) 'Cross species affective neuroscience decoding of the primal affective experiences of humans and related animals', *PLoS One*, 6: I20236.

Pansini, R. and de Ruiter, J. R. (2011) 'Observation of tool use and modification for apparent hygiene purposes in a mandrill', *Behavioural Processes*, 88: 53–5.

Parker, M., Goodwin, D., Redhead, E., and Mitchell, H. (2006) 'The effectiveness of environmental enrichment on reducing stereotypic behaviour in two captive vicugna (*Vicugna vicugna*)', *Animal Welfare*, 15: 59–62.

Parr, M. J., Bennun, L., Boucher, T., *et al.* (2009) 'Why we should aim for zero extinction', *Trends in Ecology and Evolution*, 24: 181.

Paśko, L. (2010) 'Tool-like behaviour in the sixbar wrasse, *Thalassoma hardwicke* (Bennett, 1830)', *Zoo Biology*, 29: 767–73.

Patrick, P. G., Matthews, C. E., Ayers, D. F., and Tunnicliffe, S. D. (2007) 'Conservation and education: prominent themes in zoo mission statements', *Journal of Environmental Education*, 38: 53–9.

Payne, C. L. R., Webster, T. H., and Hunt, K. D. (2008) 'Coprophagy by the semi-habituated chimpanzees of Semliki, Uganda', *Pan Africa News* 15: 29–32.

Pearce, J. M. (2008) *Animal Learning and Cognition* (3rd edition), Hove: Psychology Press.

Pearce-Kelly, P., Mace, G. M., and Clarke, D. (1995) 'The release of captive-bred snails (*Partula taeniata*) into a semi-natural environment', *Biodiversity and Conservation*, 4: 645–63.

Pearce-Kelly, P., Jones, R., Clarke, D., Walker, C., Atkin, P., and Cunningham, A. A. (1998) 'The captive rearing of threatened *Orthoptera*: a comparison of the conservation potential and practical considerations of two species' breeding programmes at the Zoological Society of London', *Journal of Insect Conservation*, 2: 201–10.

Pearson, E. L., Davis, J. M., and Litchfield, C. A. (2010) 'A case study of orang-utan and siamang behavior within a mixed-species zoo exhibit', *Journal of Applied Animal Welfare Science* 13: 330–46.

Pearson, G. L. (1977) 'Vaccine-induced canine distemper virus in black-footed ferrets', *Journal of the American Veterinary Medicine Association*, 170: 103–9.

Peeters, E. and Geers, R. (2006) 'Influence of provision of toys during transport and lairage on stress responses and meat quality of pigs', *Animal Science*, 82: 591–5.

Pennisi, E. (2001) 'Zoo's new primate exhibit to double as research lab', *Science*, 293: 1247.

Perdue, B. M., Clay, A. W., Gaalema, D. E., Maple, T. L., and Stoinski, T. S. (2012) 'Technology at the zoo: the influence of a touchscreen computer on orangutans and zoo visitors', *Zoo Biology*, 31: 27–39.

Perdue, B. M., Stoinski, T. S., and Maple, T. L. (2012) 'Using technology to educate zoo visitors about conservation', *Visitor Studies*, 15: 16–27.

Pereboom, J. J. M., Leus, K., and van Elsacker, L. (2011) 'Pro natura et scientia: zoo research at the Royal Zoological Society of Antwerp', *International Zoo Yearbook*, 45: 38–47.

Perelman, P., Johnson, W. E., Roos, C., *et al.* (2011) 'A molecular phylogeny of living primates', *PLoS Genetics* 7: e1001342.

Perkins, L. A. (1992) 'Variables that influence the activity of captive orang-utans', *Zoo Biology*, 11: 177–86.

Pessier, A. P. (2012) 'Diagnosis and control of amphibian chytridiomycosis', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 217–23.

Peterson, R. O., Jacobs, A. K., Drummer, T. D., Mech, L. D., and Smith, D. W. (2002) 'Leadership behavior in relation to dominance and reproductive status in gray wolves, *Canis lupus*', *Canadian Journal of Zoology*, 80: 1405–12.

Pickard, A. (2003) 'Reproductive and welfare monitoring for the management of *ex situ* populations', in W. Holt, A. Pickard, J. Rodger, and D. Wildt (eds), *Reproductive Science and Integrated Conservation*, Cambridge: Cambridge University Press, pp. 132–46.

Pickering, S., Creighton, E., and Stevens-Wood, B. (1992) 'Flock size and breeding success in flamingos', *Zoo Biology*, 11: 229–34.

Picq, J.-L. (2007) 'Aging affects executive functions and memory in mouse lemur primates', *Experimental Gerontology*, 42: 223–32.

Pierce, J. (2005) 'A system for mass culture of upside-down jellyfish *Cassiopea* spp as a potential food item for medusivores in captivity', *International Zoo Yearbook*, 39: 62–9.

Pinder, N. J. and Barkham, J. P. (1978) 'An assessment of the contribution of captive breeding to the conservation of rare mammals', *Biological Conservation*, 13: 187–245.

Pizzi, R. (2004) 'Slap me with a dead penguin: what we can learn from 1001 penguin post-mortems at Edinburgh Zoo', in C. Macdonald (ed.), *Proceedings of the Sixth Annual Symposium on Zoo Research*, London: BIAZA, pp. 253–5.

Plowman, A. B. (2003) 'A note on a modification of the spread of participation index allowing for unequal zones', *Applied Animal Behaviour Science*, 83: 331–6.

Plowman, A. B. (ed.) (2006) *Zoo Research Guidelines: Statistics for Typical Zoo Datasets*, London: BIAZA.

Plowman, A. B. and Knowles, L. (2003) 'Overcoming habituation in an enrichment programme for tigers', in V. J. Hare, K. E. Worley, and B. Hammond, (eds) *Proceedings of the Fifth International Conference on Environmental Enrichment*, San Diego, CA: The Shape of Enrichment, pp. 263–8.

Plowman, A. B. and Turner, I. (2001a) 'A survey and database of browse use for mammals in UK and Irish zoos', in S. Wehnelt and C. Hudson (eds), *Proceedings of the Third Annual Symposium on Zoo Research*, London: BIAZA, pp. 50–5.

Plowman, A. B. and Turner, I. (2001b) *Database of Browse Used in Federation Zoos*, London: BIAZA (CD-ROM).

Plowman, A. B. and Turner, I. (2006) 'A survey and database of browse use for mammals in UK and Irish zoos', in A. Fidgett, M. Claus, K. Eulenberger, J.-M. Hatt, I. Hume, G. Janssens, and J. Nijboer (eds), *Zoo Animal Nutrition*, Vol. III, Fürth, Germany: Filander Verlag, pp. 193–7.

Plowman, A. B., Jordan, N. R., Anderson, N., Condon, E., and Fraser, O. (2005) 'Welfare implications of captive primate population management: behavioural and psycho-social effects of female-based contraception, oestrus and male removal in hamadryas baboons (*Papio hamadryas*)', *Applied Animal Behaviour Science*, 90: 155–65.

Plowman, A. B., Hosey, G., and Stevenson, M. (2006) *Zoo Research Guidelines: Surveys and Questionnaires*, London: BIAZA.

Plowman, A., Green, K., and Taylor, L. (2008) 'Should zoo food be chopped?', *EAZA News: Zoo Nutrition Issue*, 4: 21–3.

Pochon, V. (1998) 'Mixed species exhibit for Eastern black-and-white colobus and patas monkeys', *International Zoo Yearbook*, 36: 69–73.

Polakowski, W. (1987) *Zoo Design: The Reality of Wild Illusions*, Ann Arbor, MI: University of Michigan School of Natural Sciences.

Pond, W. G., Church, D. C., Pond, K., and Schoknecht, P. A. (2005) *Basic Animal Nutrition and Feeding* (5th edn), New York: John Wiley.

Poole, T. (1999) *UFAW Handbook on the Care and Management of Laboratory Animals* (7th edn), Oxford: Blackwell Science.

Pope, C. E. (2000) 'Embryo technology in conservation efforts for endangered felids', *Theriogenology*, 53: 163–74.

Popp, J. W. (1984) 'Interspecific aggression in mixed ungulate species exhibits', *Zoo Biology*, 3: 211–19.

Pounds, J. A., Bustamante, A. R., Coloma, L. A., *et al*. (2006) 'Widespread amphibian extinctions from epidemic disease driven by global warming', *Nature*, 439: 161–7.

Povey, K. D. and Rios, J. (2002) 'Using interpretive animals to deliver affective messages in zoos', *Journal of Interpretation Research*, 7: 19–28.

Powell, D. (1995) 'Preliminary evaluation of environmental enrichment techniques for African lions (*Panthera leo*)', *Animal Welfare*, 4: 361–71.

Powell, D. M., Carlstead, K., Tarou, L. R., Brown, J. L., and Monfort, S. L. (2006) 'Effects of construction noise on behavior and cortisol levels in a pair of captive giant pandas (*Ailuropoda melanoleuca*)', *Zoo Biology*, 25: 391–408.

Powell, D., Lin, H., Carlstead, K., et al. (2008) 'Relationships between temperament, husbandry, management, and socio-sexual behavior in captive male and female giant pandas *Ailuropoda melanoleuca*' (in English), *Current Zoology*, 54: 169–75.

Preston, D. J. (1983) 'Jumbo, king of elephants', *Natural History*, 92: 80–3.

Price, D. (2000) 'Psychological and neural mechanisms of the affective dimension of pain', *Science*, 288: 1769–72.

Price, E. and Caldwell, C. A. (2007) 'Artificially generated cultural variation between two groups of captive monkeys, *Colobus guereza kikuyuensis*', *Behavioural Processes*, 74: 13–20.

Price, E. C., McGivern, A.-M., and Ashmore, L. (1991) 'Vigilance in a group of free-ranging cotton-top tamarins *Saguinus oedipus*', *Dodo: Journal of the Jersey Wildlife Preservation Trust*, 27: 41–9.

Price, E. C., Ashmore, L. A., and McGivern, A.-M. (1994) 'Reactions of zoo visitors to free-ranging monkeys', *Zoo Biology*, 13: 355–73.

Price, E. E. and Stoinski, T. S. (2007) 'Group size: determinants in the wild and implications for the captive housing of wild mammals in zoos', *Applied Animal Behaviour Science*, 103: 255–64.

Price, E. O. (1984) 'Behavioural aspects of animal domestication', *Quarterly Review of Biology*, 59: 1–32.

Pritchard, D. J., Fa, J. E., Oldfield, S., and Harrop, S. R. (2012) Bring the captive closer to the wild: re-defining the role of *ex situ* conservation. *Oryx*, 46: 18–23.

Provenza, F. D., Scott, C. B., Phy, T. S., and Lynch, J. J. (1996) 'Preference of sheep for foods varying in flavors and nutrients', *Journal of Animal Science*, 74: 2355–61.

Prunet, P., Overli, O., Douxfils, J., Bernardini, G., Kestemont, P., and Baron, D. (2012) 'Fish welfare and genomics', *Fish Physiology and Biochemistry*, 38: 43–60.

Prusky, G. T., Reidel, C., and Douglas, R. M. (2000) 'Environmental enrichment from birth enhances visual acuity but not place learning in mice', *Behavioural Brain Research*, 114: 11–15.

Pryor, K. (2002) *Don't Shoot the Dog! The New Art of Teaching and Training*, Dorking: Ringpress Books.

Puan, C. L. and Zakaria, M. (2007) 'Perception of visitors towards the role of zoos: a Malaysian perspective', *International Zoo Yearbook*, 41: 226–32.

Pullen, K. (2005) 'Preliminary comparisons of male/male interactions within bachelor and breeding groups of western lowland gorillas (*Gorilla gorilla gorilla*)', *Applied Animal Behaviour Science*, 90: 143–53.

Pusey, A. and Packer, C. (1987) 'Dispersal and philopatry', in B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Stuhsaker (eds), *Primate Societies*, Chicago, IL: University of Chicago Press, pp. 250–66.

Q

Quinn, H. and Quinn, H. (1993) 'Estimated number of snake species that can be managed by species survival plans in North America', *Zoo Biology*, 12: 243–56.

Quirke, T. and O'Riordan, R. M. (2011) 'The effect of a randomised enrichment treatment schedule on the behaviour of cheetahs (*Acinonyx jubatus*)', *Applied Animal Behaviour Science*, 135: 103–9.

Quirke, T. and O'Riordan, R. M. (2012) 'Evaluation and interpretation of the effects of environmental enrichment utilizing varying degrees of sampling effort', *Zoo Biology*, doi: 10.1002/zoo.21003. [Epub ahead of print]

R

Rabb, G. B. (1994) 'The changing roles of zoological parks in conserving biological diversity', *American Zoologist*, 34: 159–64.

Rabb, G. B. and Saunders, C. D. (2005) 'The future of zoos and aquariums: conservation and caring', *International Zoo Yearbook*, 39: 1–26.

Rabb, G. B. and Sullivan, T. A. (1995) 'Coordinating conservation: global networking for species survival', *Biodiversity and Conservation*, 4: 536–43.

Rabin, L. A. (2003) 'Maintaining behavioural diversity in captivity for conservation: natural behaviour management', *Animal Welfare*, 12: 85–94.

Rachels, J. (1976) 'Do animals have a right to liberty?', in P. Singer and T. Regan (eds), *Animal Rights and Human Obligations*, Englewood Cliffs, NJ: Prentice Hall, pp. 205–23.

Radcliffe, R. W., Czekala, N. M., and Osofsky, S. A. (1997) 'Combined serial ultrasonography and fecal progestin analysis for reproductive evaluation of the female white rhinoceros (*Ceratotherium simum simum*): preliminary results', *Zoo Biology*, 16: 445–6.

Radford, M. (2001) *Animal Welfare Law in Britain: Regulation and Responsibility*, Oxford: Oxford University Press.

Rahbeck, C. (1993) 'Captive breeding—a useful tool in the preservation of biodiversity?', *Biodiversity and Conservation*, 2: 426–37.

Rajagopal, T., Archunan, G., and Sekar, M. (2011) 'Impact of zoo visitors on the fecal cortisol levels and behaviour of an endangered species: Indian blackbuck (*Antelope cervicapra* L.)', *Journal of Applied Animal Welfare Science*, 14: 18–32.

Ralls, K., Lundrigan, B., and Kranz, K. (1987) 'Mother–young relationships in captive ungulates: spatial and temporal patterns', *Zoo Biology*, 6: 11–20.

Ramirez, K. (ed.) (1999) *Animal Training: Successful Animal Management Through Positive Reinforcement*, Chicago, IL: Shedd Aquarium Society.

Raphael, B. L. (2003) 'Chelonians (turtles, tortoises)', in M. E. Fowler and M. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 48–58.

Raven, P. H. (2002) 'Science, sustainability, and the human prospect', *Science*, 297: 954–8.

Rawlins, C. G. C. (1985) 'Zoos and conservation: the last 20 years', *Symposia of the Zoological Society of London*, 54: 59–69.

Reade, L. S. and Waran, N. K. (1996) 'The modern zoo: how do people percieve zoo animals?', *Applied Animal Behaviour Science*, 47: 109–18.

Reading, R. P. and Miller, B. J. (2007) 'Attitudes and attitude change among zoo visitors', in A. Zimmermann, M. Hatchwell, L. Dickie, and C. West (eds), *Zoos in the 21st Century: Catalysts for Conservation?*, Cambridge: Cambridge University Press, pp. 63–91.

Reaka-Kudka, M. L., Wilson, D. E., and Wilson, E. O. (eds) (1996) *Biodiversity II: Understanding and Protecting*

our *Biological Resources*, Washington, DC: Joseph Henry Press.

Réale, D. and Festa-Bianchet, M. (2003) 'Predator-induced natural selection on temperament in bighorn ewes', *Animal Behaviour*, 65: 463–70.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., and Dingemanse, N. J. (2007) 'Integrating animal temperament within ecology and evolution', *Biological Reviews*, 82: 291–318.

Redig, P. T. and Ackermann, J. (2000) 'Raptors', in T. N. Tully, M. P. C. Lawton, and G. M. Dorrestein (eds), *Avian Medicine*, Oxford: Butterworth Heinemann, pp. 180–214.

Redshaw, M. E. and Mallinson, J. J. C. (1991) 'Learning from the wild: improving the psychological and physical well-being of captive primates', *Dodo: Journal of the Jersey Wildlife Preservation Trust*, 2712: 18–26.

Reed, H. J., Wilkins, L. J., Austin, S. D., and Gregory, N. G. (1993) 'The effect of environmental enrichment during rearing on fear reactions and depopulation trauma in adult caged hens', *Applied Animal Behaviour Science*, 36: 39–46.

Rees, P. A. (2004) 'Low environmental temperature causes an increase in stereotypic behaviour in captive Asian elephants (*Elephas maximus*)', *Journal of Thermal Biology*, 29: 37–43.

Rees, P. A. (2005a) 'The EC Zoos Directive: a lost opportunity to implement the Convention on Biological Diversity', *Journal of International Wildlife Law and Policy*, 8: 51–62.

Rees, P. A. (2005b) 'Will the EC Zoos Directive increase the conservation value of zoo research?', *Oryx*, 39: 128–31.

Regal, P. (1980) 'Temperature and light requirements of captive reptiles', in J. Murphy and J. Collins (eds), *Reproductive Biology and Diseases in Captive Reptiles*, St Louis, MO: Society for the Study of Amphibians and Reptiles, pp. 79–91.

Regan, J. (2005) *The Manifesto for Zoos*, Manchester: John Regan Associates Ltd.

Regan, T. (1983) *The Case for Animal Rights*, Berkeley, CA: University of California Press.

Regan, T. (1995) 'Are zoos morally defensible?', in B. G. Norton, M. Hutchins, E. Stevens, and T. L. Maple (eds), *Ethics on the Ark: Zoos, Animal Welfare and Wildlife Conservation*, Washington, DC: Smithsonian Institute Press, pp. 38–51.

Reidarson, T. H., McBain, D. V. M., and Burch, L. (1999) 'A novel approach to the treatment of bumblefoot in penguins', *Journal of Avian Medicine and Surgery*, 13: 124–7.

Reinhardt, V. (1994a) 'Caged rhesus macaques voluntarily work for ordinary food', *Primates*, 35: 95–8.

Reinhardt, V. (1994b) 'Safe pair formation technique for previously single-caged rhesus macaques', available online at **http://www.awionline.org/Lab_animals/ biblio/tou-safe.htm**.

Reinhardt, V. (1995) 'Arguments for single-caging of rhesus macaques: are they justified?', *Animal Welfare Information Center Newsletter*, 6: 1–2.

Reinhardt, V. (2003) 'Working with rather than against macaques during blood collection', *Journal of Applied Animal Welfare Science*, 6: 189–97.

Reinhardt, V. and Reinhardt, A. (2000) 'Social enhancement for adult non-human primates in research laboratories: a review', *Lab Animal*, 29: 34–41.

Reinhardt, V. and Roberts, A. (1997) 'Effective feeding enrichment for non-human primates: a brief review', *Animal Welfare*, 6: 265–72.

Reinhardt, V., Liss, C., and Stevens, C. (1996) 'Space requirement stipulations for caged non-human primates in the United States: a critical review', *Animal Welfare*, 5: 361–72.

Reinhardt, V., Bryant, D., Kurth, B., *et al*. (1998) 'Discussion: a plea for pair-housing of adult macaques', *Laboratory Primate Newsletter*, 37: 4.

Reiss, D. (2005) 'Enriching animals while enriching science: providing choice and control to dolphins', in N. Clum, S. Silver, and P. Thomas (eds), *Seventh Conference on Environmental Enrichment*, San Diego, CA: The Shape of Enrichment, pp. 26–31.

Rendall, D. and Taylor, L. T. (1991) 'Female sexual behavior in the absence of male–male competition in captive Japanese macaques (*Macaca fuscata*)', *Zoo Biology*, 10: 319–28.

Renner, M. J. and Lussier, J. P. (2002) 'Environmental enrichment for the captive spectacled bear (*Tremarctos ornatus*)', *Pharmacology Biochemistry and Behavior*, 73: 279–83.

Rhoads, D. L. and Goldsworthy, R. J. (1979) 'The effects of zoo environments on public attitudes toward endangered wildlife', *International Journal of Environmental Studies*, 13: 283–7.

Richman, L. K. (2007) 'Elephant herpesviruses', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine* (6th edn), Philadelphia, PA: Saunders Elsevier, pp. 349–54.

Richman, L. K. and Hayward, G. S. (2012) 'Elephant herpesviruses', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 496–502.

Robbins, C. T. (1993) *Wildlife Feeding and Nutrition* (2nd edn), New York: Academic Press.

Roberts, R. L., Roytburd, L. A., and Newman, J. D. (1999) 'Puzzle feeders and gum feeders as environmental enrichment for common marmosets', *Contemporary Topics in Laboratory Animal Science*, 38: 27–31.

Robertson, D. R. (1982) 'Fish faeces as fish food on a Pacific coral-reef', *Marine Ecology Progress Series*, 7: 253–65.

Robins, J. G., and Waitt, C. D. (2011) 'Improving the welfare of captive macaques (Macaca sp.) through the use of water as enrichment', *Journal of Applied Animal Welfare Science*, 14: 75–84.

Robinson, M. H. (1989) 'The zoo that is not: education for conservation', *Conservation Biology*, 3: 213–15.

Robinson, M. H. (1996a) 'Foreword', in R. J. Hoage and W. A. Deiss (eds), *New Worlds, New Animals: From Menagerie to Zoological Park in the Nineteenth Century*, Baltimore, MD: Johns Hopkins University Press, pp. vii–xi.

Robinson, M. H. (1996b) 'The BioPark concept and the exhibition of mammals', in D. G. Kleiman, M. E. Allen, K. V. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago Press, pp. 161–6.

Roca, A. L., Georgiadis, N., Pecon-Slattery, J., and O'Brien, S. J. (2001) 'Genetic evidence for two species of elephant in Africa', *Science*, 293: 1473–7.

Rodda, G., Bock, B., Burghardt, G., and Rand, A. (1988) 'Techniques for identifying individual lizards at a distance reveal influences of handling', *Copeia*, 1988: 905–13.

Roeder, J.-J. (1980) 'Marking behaviour and olfactory recognition in genets (*Genetta genetta* L.; in Carnivora-Viverridae)', *Behaviour*, 72: 200–10.

Roeder, J.-J. (1983) 'Études des interactions sociales entre mâle et femelle chez la genette (*Genetta genetta* L.): relations entre marquage olfactif et agression', *Zeitschrift für Tierpsychologie*, 61: 293–310.

Roeder, J.-J. (1984) 'Ontogenèse des systèmes de communication chez la genette (*Genetta genetta* L.)', *Behaviour*, 90: 259–301.

Rollin, B. E. (1992) *Animal Rights and Human Morality*, New York: Prometheus Books.

Romero, T. and Aureli, F. (2007) 'Spatial association and social behaviour in zoo-living female ring-tailed coatis (*Nasua nasua*)', *Behaviour*, 144: 179–93.

Rosier, R. L. and Langkilde, T (2011) 'Does environmental enrichment really matter? A case study using the eastern fence lizard, *Sceloporus undulatus*', *Applied Animal Behaviour Science*, 131: 71–6.

Ross, S. R. (2006) 'Issues of choice and control in the behaviour of a pair of captive polar bears (*Ursus maritimus*)', *Behavioural Processes*, 73: 117–20.

Ross, S. R. and Gillespie, K. L. (2009) 'Influences on visitor behavior at a modern immersive zoo exhibit', *Zoo Biology*, 28: 462–72.

Ross, S. R. and Lukas, K. E. (2005) 'Zoo visitor behavior at an African ape exhibit', *Visitor Studies Today*, 8: 4–12.

Ross, S. R. and Lukas, K. E. (2006) 'Use of space in a non-naturalistic environment by chimpanzees (*Pan troglodytes*) and lowland gorillas (*Gorilla gorilla gorilla*)', *Applied Animal Behaviour Science*, 96: 143–52.

Ross, S. R., Schapiro, S. J., Hau, J., and Lukas, K. E. (2009). 'Space use as an indicator of enclosure appropriateness: a novel measure of captive animal welfare', *Applied Animal Behaviour Science*, 121: 42–50.

Ross, S. R., Wagner, K. E., Schapiro, S. J., Hau, J., and Lukas, K. E. (2011) 'Transfer and acclimatization effects on the behavior of two species of African great ape (*Pan troglodytes* and *Gorilla gorilla gorilla*) moved to a novel and naturalistic zoo environment', *International Journal of Primatology*, 32: 99–117.

Rothfels, N. (2002) *Savages and Beasts: The Birth of the Modern Zoo*, Baltimore, MD: Johns Hopkins University Press.

Rothschild, B. M., Rothschild, C., and Woods, R. J. (2001) 'Inflammatory arthritis in canids: spondyloarthropy', *Journal of Zoo Wildlife Medicine*, 32: 58–64.

Roush, R. S., Burkhardt, R., Converse, L., *et al*. (1992) 'Comment on "Are alarming events good for captive monkeys?"', *Applied Animal Behaviour Science*, 33: 291–3.

Routman, E., Ogden, J., and Winsten, K. (2010) 'Visitors, conservation learning, and the design of zoo and aquarium experiences', in D. G. Kleiman, K. V. Thompson, and C. Kirk Baer (editors). *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: University of Chicago Press, pp 137–50.

Rowland, D. L., Helgeson, V. S., and Cox, C. C. (1984) 'Temporal patterns of parturition in mammals in captivity', *Chronobiologica*, 11: 31–9.

Rushen, J. (1993) 'The "coping" hypothesis of stereotypic behaviour', *Animal Behaviour*, 45: 613–15.

Rushen, J. (2003) 'Changing concepts of farm animal welfare: bridging the gap between applied and basic research', *Applied Animal Behaviour Science*, 81: 199–214.

Rushen, J. and Depassillé, A. M. B. (1992) 'The scientific assessment of the impact of housing on animal welfare: a critical review', *Canadian Journal of Animal Science*, 72: 721–43.

Russel, A. (1984) 'Body condition scoring of sheep', *In Practice*, 6: 91–3.

Russow, L.-M. (2002) 'Ethical implications of the human–animal bond in the laboratory', *ILAR Journal*, 43: 33–7.

Rutherford, K. (2002) 'Assessing pain in animals', *Animal Welfare*, 11: 31–53.

Ruxton, G. and Colegrave, N. (2010) *Experimental Design for the Life Sciences* (3rd edn), Oxford: Oxford University Press.

Ryan, S., Thompson, S., Roth, A., and Gold, K. (2002) 'Effects of hand-rearing on the reproductive success of western lowland gorillas in North America', *Zoo Biology*, 21: 389–401.

Ryder, O. A. (1986) 'Species conservation and systematics: the dilemma of subspecies', *Trends in Ecology and Evolution*, 1: 9–10.

Ryder, O. A. and Feistner, A. T. C. (1995) 'Research in zoos: a growth area in conservation', *Biodiversity and Conservation*, 4: 671–7.

S

Sainsbury, D. (1998) *Animal Health* (2nd edn), London: Blackwell Science.

Sales, G. D., Milligan, S. R., and Khirnykh, K. (1999) 'Sources of sound in the laboratory animal environment: a survey of the sounds produced by procedures and equipment', *Animal Welfare*, 8: 97–115.

Samour, J. H. (ed.) (2000), *Avian Medicine*, Amsterdam: Elsevier.

Sambrook, T. D. and Buchanan-Smith, H. M. (1997) 'Control and complexity in novel object enrichment', *Animal Welfare*, 6: 207–16.

Sanderson, S. (2007) 'Appendix A: Contraception', in V. Melfi (ed.) *Proceedings of the Eighth European Endangered Species Programme (EEP) Studbook for Sulawesi Crested Black Macaque (*Macaca nigra*)*, Paignton Zoo Environmental Park, pp. 51–4.

Sanderson, S. (2012) 'Bluetongue: lessons from the European outbreak 2006–2009', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 573–80.

Sanderson, S., Fidgett, A. L., and Fletcher, E. (2004) 'The effect of food presentation on the mortality rates and reproductive success of a colony of Rodrigues fruit bats (*Pteropus rodricensis*)', in *Proceedings of the European Association of Zoo and Wildlife Veterinarians Fifth Scientific Meeting*, Liebefeld-Berne, Switzerland: EAZWV, pp. 13–19.

Sannen, A., van Elsacker, L., and Eens, M. (2004) 'Effect of spatial crowding on aggressive behaviour in a bonobo colony', *Zoo Biology*, 23: 383–95.

Saskia, J. and Schmid, H. (2002) 'Effect of feeding boxes on the behaviour of stereotyping Amur tigers (*Panthera tigris altaica*) in the Zurich Zoo, Zurich, Switzerland', *Zoo Biology*, 21: 573–84.

Savage, A., Rice, J. M., Brangan, J. M., Martini, D. P., Pugh, J. A., and Miller, C. D. (1994) 'Performance of African elephants (*Loxodonta africana*) and California sea lions (*Zalophus californianus*) on a two-choice object discrimination task', *Zoo Biology*, 13: 69–75.

Savastano, G., Hanson, A., and McCann, C. (2003) 'The development of an operant conditioning training program for New World primates at the Bronx Zoo', *Journal of Applied Animal Welfare Science*, 6: 247–61.

Saxby, A., Adams, L., Snellgrove, D., Wilson, R. W., and Sloman, K. A. (2010) 'The effect of group size on the behaviour and welfare of four fish species commonly kept in home aquaria', *Applied Animal Behaviour Science* 125: 195–205.

Schaaf, C. (1984) 'Animal behaviour and the captive management of wild mammals: a personal view', *Zoo Biology*, 310: 373–7.

Schafer, E. H. (1968) 'Hunting parks and animal enclosures in Ancient China', *Journal of the Economic and Social History of the Orient*, 11: 318–43.

Schaffer, N., Beehler, B., Jeyendran, R. S., and Balke, B. (1990) 'Methods of semen collection in an ambulatory greater one-horned rhinoceros (*Rhinoceros unicornis*)', *Zoo Biology*, 9: 211–21.

Schaffner, C. M. and Smith, T. E. (2005) 'Familiarity may buffer the adverse effects of relocation on marmosets (*Callithrix kuhlii*): preliminary evidence', *Zoo Biology*, 24: 93–100.

Schapiro, S. J., Bloomsmith, M. A., Suarez, S. A., and Porter, L. M. (1997) 'A comparison of the effects of simple versus complex environmental enrichment on the behaviour of group-housed, subadult rhesus macaques', *Animal Welfare*, 6: 17–28.

Schapiro, S. J., Perlman, J. E., and Boudreau, B. A. (2001) 'Manipulating the affiliative interactions of group-housed rhesus macaques using positive reinforcement training techniques', *American Journal of Primatology*, 55: 137–49.

Schapiro, S. J., Bloomsmith, M. A., and Laule, G. E. (2003) 'Positive reinforcement training as a technique to alter non-human primate behaviour: quantitative assessments of effectiveness', *Journal of Applied Animal Welfare Science*, 6: 175–87.

Scharmann, C. and van Hooff, J. (1986) 'Reproductive strategies of the orang-utan: new data and a reconsideration of existing sociosexual models', *International Journal of Primatology*, 7: 265–87.

Schiml, P. A., Mendoza, S. P., Saltzman, W., Lyons, D. M., and Mason, W. A. (1996) 'Seasonality in squirrel monkeys (*Saimiri sciureus*): social facilitation by females', *Physiology and Behavior*, 60: 1105–13.

Schmid, J., Heistermann, M., Ganslosser, U., and Hodges, J. K. (2001) 'Introduction of foreign female Asian elephants (*Elephas maximus*) into an existing group: behavioural reactions and changes in cortisol levels', *Animal Welfare*, 10: 357–72.

Schmidt-Nielsen, K. (1997) *Animal Physiology: Adaptation and Environment*, Cambridge: Cambridge University Press.

Schmitt, D. L. (2003) 'Proboscidea (Elephants)', in M. E. Fowler and M. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Elsevier Saunders, pp. 541–50.

Schorger, A. W. (1955) *The Passenger Pigeon: Its Natural History and Extinction*. Madison, WI: University of Wisconsin Press (reprinted in paperback, 2004, by Blackburn Press).

Schramm, H. (2011). *Looking at People Looking at Animals: An International Bibliography on Visitor Experience Studies and Exhibit Evaluation in Zoos and Aquariums.* EAZA Education Committee, available at **www.eaza.net/activities/education/ Documents**.

Schreck, C. B. (2010) 'Stress and fish reproduction: the roles of allostasis and hormesis', *General and Comparative Endocrinology*, 165: 549–56.

Schulkin, J. (2003) *Rethinking Homeostasis: Allostatic Regulation in Physiology and Pathophysiology*, Cambridge, MA: MIT Press.

Schulte-Hostedde, A. I., Zinner, B., Millar, J. S., and Hickling, G. J. (2005) 'Restitution of mass-size residuals: validating body condition indices', *Ecology*, 86: 155–63.

Schwabe, C. W. (1984) *Veterinary Medicine and Human Health* (3rd edn), Baltimore, MD: Williams & Wilkins.

Schwaibold, U. and Pillay, N. (2001) 'Stereotypic behaviour is genetically transmitted in the African striped mouse *Rhabdomys pumilio*', *Applied Animal Behaviour Science*, 74: 273–80.

Schwartzkopf-Genswein, K. S., Stookey, J. M., and Welford, R. (1997) 'Behavior of cattle during hot-iron and freeze branding and the effects on subsequent handling ease', *Journal of Animal Science*, 75: 2064–72.

Schwartzkopf-Genswein, K. S., Huisma, C., and McAllister, T. A. (1999) 'Validation of a radio frequency identification system for monitoring the feeding patterns of feedlot cattle', *Livestock Production Science*, 60: 27–31.

Schwitzer, C. and Kaumanns, W. (2001) 'Body weights of ruffed lemurs (*Varecia variegata*) in European zoos, with reference to the problem of obesity', *Zoo Biology*, 20: 261–9.

Scott, G. W., Hull, S. L., and Rollinson, D. J. (1999a) 'Surface breaking behaviour in a population of captive rays *Raja*: the expression of a need to forage?', *Aquarium Sciences and Conservation*, 2: 161–9.

Scott, G. W., Rollinson, D. J., and Hull, S. L. (1999b) 'Modification in feeding regime reduces the performance of surface breaking behaviour in a population of captive rays (*Raja*)', *Aquarium Sciences and Conservation*, 2: 171–4.

Scott, L., Pearce, P., Fairhall, S., Muggleton, N., and Smith, J. (2003) 'Training non-human primates to cooperate with scientific procedures in applied biomedical research', *Journal of Applied Animal Welfare Science*, 6: 199–207.

Scott Mills, L. (2006) *Conservation of Wildlife Populations, Demography, Genetics, and Management*, Chichester: Wiley–Blackwell.

Scruton, D. M. and Herbert, J. (1972) 'The reaction of groups of captive talapoin monkeys to the introduction of male and female strangers of the same species', *Animal Behaviour*, 20: 463–73.

Seal, U. S. (1991) 'Life after extinction', *Symposium of the Zoological Society of London*, 62: 39–55.

Seebeck, J. and Booth, R. (1996) 'Eastern barred bandicoot recovery: the role of the veterinarian in the management of endangered species', *Australian Veterinary Journal*, 73: 81–3.

Segovia, G., Yague, A. G., Garcia-Verdugo, J. M., and Mora, F. (2006) 'Environmental enrichment promotes neurogenesis and changes the extracellular concentrations of glutamate and GABA in the hippocampus of aged rats', *Brain Research Bulletin*, 70: 8–14.

Seidensticker, J. and Doherty, J. (1996) 'Integrating animal behaviour and exhibit design', in D. Kleiman, M. Allen, K. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity*, Chicago, IL: Chicago University Press, pp. 180–90.

Sellinger, R. L. and Ha, J. C. (2005) 'The effects of visitor density and intensity on the behaviour of two captive jaguars (*Panthera onca*)', *Journal of Applied Animal Welfare Science*, 8: 233–44.

Seltzer, L. J. and Ziegler, T. E. (2007) 'Non-invasive measurement of small peptides in the common marmoset (*Callithrix jacchus*): a radiolabeled clearance study and endogenous excretion under varying conditions', *Hormones and Behavior*, 51: 436–42.

Selye, H. (1973) 'The evolution of the stress concept', *American Scientist*, 61: 692–9.

Semple, S. (2002) 'Analysis of research projects conducted in Federation collections to 2000', *Federation Research Newsletter*, 3: 3.

Seres, M., Aureli, F., and de Waal, F. B. M. (2001) 'Successful formation of a large chimpanzee group out of two preexisting subgroups', *Zoo Biology*, 20: 501–15.

Sha, J., Han, S., Marlena, D., and Kee, J. (2012) 'Effects of single-use and group-use enrichment on stereotypy and intragroup aggressive and affiliative behaviors of a social group of squirrel monkeys (*Saimiri sciureus*) at the Singapore Zoo', *Journal of Applied Animal Welfare Science*, 15: 358–71.

Shackley, M. (1996) *Wildlife Tourism*, London: Routledge.

Shaffer, M. L. (1981) 'Minimum population sizes for species conservation', *Bioscience* 31: 131–4.

Shannon, G. (2005) 'The effects of sexual dimorphism on the movements and foraging ecology of the African elephant', unpublished PhD thesis, School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban.

Shepherdson, D. (1991) 'A wild time at the zoo: practical enrichment for zoo animals', *Annual Conference of the American Association of Zoological Parks and Aquariums*, San Diego, CA: AAZPA, pp. 413–20.

Shepherdson, D. (1994) 'The role of environmental enrichment in the captive breeding and reintroduction of endangered species', in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner (eds), *Creative Conservation: Interactive Management of Wild and Captive Animals*, London: Chapman & Hall, pp. 167–77.

Shepherdson, D. (1998) *Second Nature: Environmental Enrichment for Captive Animals*, Washington, DC: Smithsonian Books.

Shepherdson, D. J., Carlstead, K. C., Mellen, J., and Seidensticker, J. (1993) 'The influence of food presentation on the behavior of small cats in confined environments', *Zoo Biology*, 12: 203–16.

Shepherdson, D., Carlstead, K. C., and Wielebnowski, N. (2004) 'Cross-institutional assessment of stress responses in zoo animals using longitudinal monitoring of faecal corticoids and behaviour', *Animal Welfare*, 13: 105–13.

Sheppard, C. (1995) 'Propagation of endangered birds in US institutions. How much space is there?', *Zoo Biology*, 14: 197–210.

Sheppard, C. and Dierenfeld, E. (2002) 'Iron storage disease in birds: speculation on etiology and implications for captive husbandry', *Journal of Avian Medicine and Surgery*, 16: 192–7.

Sherrill, J., Spelman, L. H., Reidel, C. L., and Montali, R. J. (2000) 'Common cuttlefish (*Sepia officinalis*) mortality at the National Zoological Park: implications for clinical management', *Journal of Zoo and Wildlife Medicine*, 31: 523–31.

Sherwin, C. (2001) 'Can invertebrates suffer? Or, how robust is argument-by-analogy?', *Animal Welfare*, 10: 103–18.

Shi, Y. and Yokoyama, S. (2003) 'Molecular analysis of the evolutionary significance of ultraviolet vision in vertebrates', *Proceedings of the National Academy of Sciences of the USA*, 100: 8308–13.

Shine, C., Shine, N., Shine, R., and Slip, D. (1988) 'Use of subcaudal scale anomalies as an aid in recognizing individual snakes', *Herpetological Review*, 19: 79.

Shyne, A. and Block, M. (2010) 'The effects of husbandry training on stereotypic pacing in captive African wild dogs (*Lycaon pictus*)', *Journal of Applied Animal Welfare Science* 13: 56–65.

Sibley, C. G. and Monroe, B. L., Jr (1990) *Distribution and Taxonomy of the Birds of the World*, New Haven, CT: Yale University Press.

Sibley, C. G. and Monroe, B. L., Jr (1993) *Supplement to Distribution and Taxonomy of the Birds of the World*, New Haven, CT: Yale University Press.

Signal, T. D. and Taylor, N. (2006) 'Attitudes to animals in the animal protection community compared to a normative community sample', *Society and Animals*, 14: 265–74.

Sigsgaard, S. (2009). Conservation in zoo shops today and in the future: a case study and discussion. *International Zoo Yearbook*, 43: 91–102.

Sigurdson, C. J. and Miller, M. W. (2003) 'Other animal prion diseases', *British Medical Bulletin*, 66: 199–212.

Sih, A., Bell, A., and Chadwick Johnson, J. (2004) 'Behavioural syndromes: an ecological and evolutionary overview', *Trends in Ecology and Evolution*, 19: 372–8.

Silk, J. (1989) 'Social behaviour in evolutionary perspective', in B. Smuts, D. Cheney, R. Seyfarth, R. Wrangham, and T. Strusaker (eds), *Primate Societies*, Chicago, IL: Chicago University Press, pp. 318–29.

Silver, S. C., Ostro, L. E. T., Yeager, C. P., and Dierenfeld, E. S. (2000) 'Phytochemical and mineral components of foods consumed by black howler monkeys (*Alouatta pigra*) at two sites in Belize', *Zoo Biology*, 19: 95–109.

Simeone, A., Wilson, R. P., Knauf, G., Knauf, W., and Schützendübe, J. (2002) 'Effects of attached data-loggers on the activity budgets of captive Humboldt penguins', *Zoo Biology*, 21: 365–73.

Simmonds, M. P. (2006) 'Into the brains of whales', *Applied Animal Behaviour Science*, 100: 103–16.

Singer, P. (1975) *Animal Liberation*, New York: New York Review of Books.

Singer, P. (2009) *Animal Liberation: The Definitive Classic of the Animal Movement* New York: HarperCollins.

Singer, P. and Regan, T. (1999) *Animal Rights and Human Obligations*, Upper Saddle River, NJ: Prentice Hall.

Sinn, D. L., Perrin, N. A., Mather, J. A., and Anderson, R. C. (2001) Early temperamental traits in an octopus (*Octopus bimaculoides*). *Journal of Comparative Psychology*, 115, 351–64.

Skinner, B. (1938) *The Behavior of Organisms: An Experimental Analysis*, New York: Appleton-Century.

Sklan, D., Melamed, D., and Friedman, A. (1994) 'The effects of varying levels of dietary vitamin A on immune response in the chick', *Poultry Science*, 73: 843–7.

Slocombe, K. E. and Zuberbühler, K. (2005) 'Functionally referential communication in a chimpanzee', *Current Biology*, 15: 1779–84.

Smith, A., Lindburg, D. G., and Vehrencamp, S. (1989) 'Effect of food preparation on feeding behavior of lion-tailed macaques', *Zoo Biology*, 8: 57–65.

Smith, E. J., Partridge, J. C., Parsons, K. N., *et al*. (2002) 'Ultraviolet vision and mate choice in the guppy (*Poecilia reticulata*)', *Behavioural Ecology*, 13: 11–19.

Smith, L. (2013) 'Visitors or visits? An examination of zoo visitor numbers using the case study of Australia', *Zoo Biology*, 32: 37–44.

Smith, L., Weiler, B. and Ham, S. (2011) 'The rhetoric versus the reality: a critical examination of the zoo proposition', in W. Frost (ed) *Zoos and Tourism: Conservation, Education, Entertainment?*, Bristol: Channel View Publications, pp. 59–68.

Smith, S. (2006) 'Environmental enrichment plan for elasmobranchs at Shark Bay, Sea World, Gold Coast, Australia', in *Proceedings of the First Australasian Regional Environmental Enrichment Conference*, San Diego, CA: Shape of Enrichment.

Smith, T. (2004) *Zoo Research Guidelines: Monitoring Stress in Zoo Animals*, London: BIAZA.

Sneddon, I. A., Beattie, V. E., Dunne, L., and Neil, W. (2000) 'The effect of environmental enrichment on learning in pigs', *Animal Welfare*, 9: 373–83.

Sneddon, L. (2003) 'The evidence for pain in fish: the use of morphine as an analgesic', *Applied Animal Behaviour Science*, 83: 153–62.

Sneddon, L. U. (2009) 'Pain perception in fish: indicators and endpoints', *ILAR Journal*, 50: 338–42.

Sodhi, N. S., Bickford, D., Diesmos, A. C., *et al*. (2008) 'Measuring the meltdown: drivers of global amphibian extinction and decline', *PLoS One*, 3: e1636.

Soloman, N. G. and French, J. A. (2007) *Cooperative Breeding in Mammals*, Cambridge: Cambridge University Press.

Sommerfeld, R., Bauert, M., Hillmann, E., and Stauffacher, M. (2006) 'Feeding enrichment by self-operated food boxes for white-fronted lemurs (*Eulemur fulvus albifrons*) in the Masoala exhibit of the Zurich Zoo', *Zoo Biology*, 25: 145–54.

Soulé, M., Gilpin, M., Conway, W., and Foose, T. (1986) 'The millenium ark: how long a voyage, how many staterooms, how many passengers?', *Zoo Biology*, 5: 101–13.

Southwick, C. H. (1967) 'An experimental study of intragroup agonistic behaviour in rhesus monkeys (*Macaca mulatta*)', *Behaviour*, 28: 182–209.

Sowell, B. F., Bowman, J. G. P., Branine, M. E., and Hubbert, M. E. (1998) 'Radio frequency technology to measure feeding behavior and health of feedlot steers', *Applied Animal Behaviour Science*, 59: 277–84.

Spalton, J. A., Brend, S. A., and Lawrence, M. W. (1999) 'Arabian oryx reintroduction in Oman: successes and setbacks', *Oryx*, 33: 168–75.

Speakman, J. (2005) 'Review: body size, energy metabolism and lifespan', *Journal of Experimental Biology*, 218: 1717–30.

Spelman, L. H. (1999) 'Vermin control', in M. E. Fowler and M. E. Miller (eds), *Zoo and Wild Animal Medicine: Current Therapy* (4th edn), Philadelphia, PA: Elsevier Saunders, pp. 114–20.

Spelman, L. H., Osborn, K. G., and Anderson, M. P. (1989) 'Pathogenesis of hemosiderosis in lemurs: role of dietary iron, tannin, and ascorbic acid', *Zoo Biology*, 8: 239–51.

Spencer, W. and Spencer, J. (2006) *Management Guideline Manual for Invertebrate Live Food Species*, Amsterdam: EAZA Terrestrial Invertebrate TAG.

Spinelli, J. and Markowitz, H. (1985) 'Prevention of cage-associated distress', *Lab Animal*, 14: 19–28.

Spinka, M. (2006) 'How important is natural behaviour in animal farming systems?', *Applied Animal Behaviour Science*, 100: 117–28.

Spotte, S. (1992) *Captive Seawater Fishes: Science and Technology*, New York: John Wiley.

Spraker, T. R. (2003) 'Spongiform encephalopathy', in M. E. Fowler and M. E. Miller (eds), *Zoo and Wild Animal Medicine: Current Therapy* (5th edn), Philadelphia, PA: Elsevier Saunders, pp. 741–5.

Spring, S. E., Clifford, J. O., and Tomko, D. L. (1997) 'Effect of environmental enrichment devices on behaviors of single- and group-housed squirrel monkeys (*Saimiri sciureus*)', *Contemporary Topics in Laboratory Animal Science*, 36: 72–5.

Springer, M. S. and de Jong, W. W. (2001) 'Phylogenetics: which mammalian supertree to bark up?', *Science*, 291: 1709–11.

Stacey, P. B. and Koenig, W. D. (1990) *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior*, Cambridge: Cambridge University Press.

Stamps, J. A., Groothuis, T. G. G. (2010) 'The development of animal personality: relevance, concepts and perspectives' *Biological Reviews*, 85, 301–25

Stanley, M. E. and Aspey, W. P. (1984) 'An ethometric analysis in a zoological garden: modification of ungulate behavior by the visual presence of a predator', *Zoo Biology*, 3: 89–109.

Stanley Price, M. R. (1991) 'A review of mammal reintroductions, and the role of the reintroduction specialist group of IUCN/SSC', *Symposium of the Zoological Society of London*, 62: 9–25.

Stanley Price, M. R. and Fa, J. E. (2007) 'Reintroductions from zoos: a conservation guiding light or a shooting star?', in A. Zimmerman, M. Hatchwell, L. Dickie, and C. West (eds), *Zoos in the 21st Century: Catalysts for Conservation?*, Cambridge: Cambridge University Press, pp. 155–77.

Steele, K. M., Linn, M. J., Schoepp, R. J., et al. (2000) 'Pathology of fatal West Nile virus infections in native and exotic birds during the 1999 outbreak in New York City, New York', *Veterinary Pathology*, 37: 208–24.

Sterling, E., Lee, J., and Wood, T. (2007) 'Conservation education in zoos: an emphasis on behavioral change', in A. Zimmerman, M. Hatchwell, L. Dickie, and C. West (eds), *Zoos in the 21st Century: Catalysts for Conservation?*, Cambridge: Cambridge University Press, pp. 37–50.

Sterling, P. and Eyer, J. (1988) 'Handbook of life stress, cognition and health', in S. Fisher and J. Reason (eds), *Allostasis: A New Paradigm to Explain Arousal Pathology*, New York: John Wiley, pp. 629–49.

Sternicki, T., Szablewski, P., and Szwaczkowski, T. (2003) 'Inbreeding effects on lifetime in David's deer (*Elaphurus davidianus*, Milne Edwards 1866) population', *Journal of Applied Genetics*, 44: 175–83.

Stevens, C. E. and Hume, I. D. (1995). *Comparative Physiology of the Vertebrate Digestive System* (2nd edn), Cambridge: Cambridge University Press.

Stevens, E. F. (1991) 'Flamingo breeding: the role of group displays', *Zoo Biology*, 10: 53–63.

Stevens, E. F. and Pickett, C. (1994) 'Managing the social environments of flamingos for reproductive success', *Zoo Biology*, 13: 501–7.

Stevenson, M. (1983) 'The captive environment: its effect on exploratory and related behavioural responses in wild animals', in J. Archer and L. Birkexs (eds), *Exploration in Animals and Man*, New York: Van Nostrand–Reinhold, pp. 176–97.

Stevenson, M. (2008) *BIAZA Questionnaire: What It Is For and What It Achieves*, London: BIAZA.

Stevenson, M. (2010). 'Setting standards for evaluation of captive facilities: Europe', in D. G. Kleiman, K. V. Thompson, and C. Kirk Baer (eds), *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: University of Chicago Press, pp. 31–4.

Stevenson, M. and Walter, O. (2006) *Management Guidelines for the Welfare of Zoo Animals: Elephants* (Loxodonta africana *and* Elephas maximus) (2nd edn), London: BIAZA.

St Louis, V., Barlow, J., and Sweerts, J. (1989) 'Toenail-clipping: a simple technique for marking individual nidicolous chicks', *Journal of Field Ornithology*, 60: 211–15.

Stoinski, T. S., Beck, B., Bowman, M., and Lehnhardt, J. (1997) 'The Gateway zoo program: a recent initiative in golden lion tamarin reintroduction', *American Society of Primatologists, Special Topics in Primatology*, 1: 29–41.

Stoinski, T. S., Lukas, K. E., and Maple, T. L. (1998) 'A survey of research in North American zoos and aquariums', *Zoo Biology*, 17: 167–80.

Stoinski, T. S., Daniel, E., and Maple, T. L. (2000) 'A preliminary study of the behavioral effects of feeding enrichment on African elephants', *Zoo Biology*, 19: 485–93.

Stoinski, T. S., Hoff, M. P., Lukas, K. E., and Maple, T. L. (2001) 'A preliminary behavioral comparison of two captive all-male gorilla groups', *Zoo Biology*, 20: 27–40.

Stoinski, T. S., Allen, M. T., Bloomsmith, M. A., Forthman, D. L., and Maple, T. L. (2002) 'Educating zoo visitors about complex environmental issues. Should we do it and how?', *Curator*, 45: 129–43.

Stoinski, T. S., Beck, B. B., Bloomsmith, M. A., and Maple, T. L. (2003) 'A behavioural comparison of captive-born, reintroduced golden lion tamarins and their wild-born offspring', *Behaviour*, 140: 137–60.

Stoinski, T. S., Drayton, L. A., and Price, E. E. (2011) 'Evidence of social learning in black-and-white ruffed lemurs (*Varecia variegata variegata*)', *Biology Letters*, 7: 376–9.

Stolba, A. and Wood-Gush, D. (1984) 'The identification of behavioural key features and their incorporation into a housing design for pigs', *Annales de Recherches Veterinaires*, 15: 287–98.

Stone, R. (2003) 'Foreword', in W. Holt, A. Pickard, J. Rodger, and D. Wildt (eds), *Reproductive Science and Integrated Conservation*, Cambridge: Cambridge University Press, pp. xiii–xv.

Storms, T. N., Clyde, V. L., Munson, L., and Ramsay, E. C. (2003) 'Blastomycosis in non-domestic felids', *Journal of Zoo and Wildlife Medicine*, 34: 231–8.

Straughan, R. (2003) *Ethics, Morality and Crop Biotechnology*, Report sponsored by the Biotechnology and Biological Sciences Research Council (BBSRC), available online at **http://www.bbsrc.ac.uk/organisation/ policies/position/public_interest/animal_biotechnology.pdf**.

Strouhal, E. (1992) *Life in Ancient Egypt*, Cambridge: Cambridge University Press.

Stuart, S. N. (1991) 'Re-introductions: to what extent are they needed?', *Symposium of the Zoological Society of London*, 62: 27–37.

Stuart, S. N., Chanson, J. S., Cox, N. A., *et al*. (2004) 'Status and trends of amphibian declines and extinctions worldwide', *Science*, 306: 1783–6.

Sulser, C. E., Steck, B. L., and Baur, B. (2008) 'Effects of construction noise on behaviour of and exhibit use by snow leopards *Uncia uncia* at Basel Zoo', *International Zoo Yearbook*, 42: 199–205.

Sunquist, F. (1995) 'End of the ark?', *International Wildlife*, 25: 23–9.

Sutherland, W., Newton, I., and Green, R. (2004) *Bird Ecology and Conservation: A Handbook of Techniques.* Oxford: Oxford University Press.

Swain, D. L., Wilson, L. A., and Dickinson, J. (2003) 'Evaluation of an active transponder system to monitor spatial and temporal location of cattle within patches of a grazed sward', *Applied Animal Behaviour Science*, 84: 185–95.

Swaisgood, R. R. (2007) 'Current status and future directions of applied behavioral research for animal welfare and conservation', *Applied Animal Behaviour Science*, 102: 139–62.

Swaisgood, R. R. and Shepherdson, D. J. (2005) 'Scientific approaches to enrichment and stereotypies in zoo animals: what's been done and where should we go next?', *Zoo Biology*, 24: 499–518.

Swaisgood, R. R., White, A. M., Zhou, X. P., *et al*. (2001) 'A quantitative assessment of the efficacy of an environmental enrichment programme for giant pandas', *Animal Behaviour*, 61: 447–57.

Swaisgood, R. R. and Shepherdson, D. J. (2006) 'Environmental enrichment as a strategy for mitigating stereotypies in zoo animals: a literature review and meta-analysis', in G. J. Mason and J. Rushen (eds), *Stereotypic*

Animal Behaviour: Fundamentals and Applications to Welfare, Wallingford: CABI Publishing, pp. 256–85.

Swan, G., Naidoo, V., Cuthbert, R., *et al*. (2006) 'Removing the threat of diclofenac to critically endangered Asian vultures', *PLoS Biology*, 4: e66.

Swanson, W. F., Johnson, W. E., Cambre, R. C., *et al*. (2003) 'Reproductive status of endemic felid species in Latin American zoos and implications for *ex situ* conservation', *Zoo Biology*, 22: 421–41.

Swenson, J., Wallin, K., Ericsson, G., Cederlund, G., and Sandegren, F. (1999) 'Effects of ear-tagging with radiotransmitters on survival of moose calves', *Journal of Wildlife Management*, 63: 354–8.

Sykes, J. B. (ed.) (1977) *Concise Oxford Dictionary of Current English* (6th edn), Oxford: Oxford University Press.

Szokalski, M. S., Litchfield, C. A., and Foster, W. K. (2012a) 'Enrichment for captive tigers (*Panthera tigris)*: current knowledge and future directions, *Applied Animal Behaviour Science*, 139: 1–9.

Szokalski, M. S., Litchfield, C. A., and Foster, W. K. (2012b) 'What can zookeepers tell us about interacting with big cats in captivity', *Zoo Biology*, doi: 10.1002/zoo.21040 [Epub ahead of print].

T

Taber, A. and Macdonald, D. W. (1992) 'Spatial organisation and monogamy in the mara, *Dolichotis patagonum*', *Journal of Zoology*, 227: 417–38.

Taberlet, T. and Bouvet, J. (1991) 'A single plucked feather as a source of DNA for bird genetic studies', *Auk*, 108: 959–60.

Tarou, L. R., Bashaw, M. J., and Maple, T. L. (2000) 'Social attachment in giraffe: response to social separation', *Zoo Biology*, 19: 41–51.

Tarou, L. R., Bashaw, M. J., and Maple, T. L. (2003) 'Failure of a chemical spray to significantly reduce stereotypic licking in a captive giraffe', *Zoo Biology*, 22: 601–7.

Tarou, L. R., Kuhar, C. W., Adcock, D., Bloomsmith, M. A., and Maple, T. L. (2004) 'Computer-assisted enrichment for zoo-housed orang-utans (*Pongo pygmaeus*)', *Animal Welfare*, 13: 445–53.

Taubert, J. (2010) 'Evidence of human-like, holistic face processing in spider monkeys (*Ateles geoffroyi*)', *Journal of Comparative Psychology*, 124: 57–65.

Taylor, A. C. (2003) 'Assessing the consequences of inbreeding for population fitness: past challenges

and future prospects', in W. Holt, A. Pickard, J. Rodger, and D. Wildt (eds), *Reproductive Science and Integrated Conservation*, Cambridge: Cambridge University Press, pp. 67–81.

Taylor, J. J. (1984) 'Iron accumulation in avian species in captivity', *Dodo: Journal of the Jersey Wildlife Preservation Trust*, 21: 126–31.

Terranova, C. J. and Coffman, B. S. (1997) 'Body weights of wild and captive lemurs', *Zoo Biology*, 16: 17–30.

Testa, J. W. and Rothery, P. (1992) 'Effectiveness of various cattle ear tags as markers for Weddell seals', *Marine Mammal Science*, 8: 344–53.

Tetley, C. L. and O'Hara, S. J. (2012) 'Ratings of animal personality as a tool for improving the breeding, management and welfare of zoo mammals', *Animal Welfare*, 21: 463–76.

Therrien, C. L., Gaster, L., Cunningham-Smith, P., and Manire, C. A. (2007) 'Experimental evaluation of environmental enrichment of sea turtles', *Zoo Biology*, 26: 407–16.

Thiermann, A. and Babcock, S. (2005) 'Animal welfare and international trade', *Science and Technology Review*, 24: 747–55.

Thodberg, K., Jensen, K. H., Herskin, M. S., and Jorgensen, E. (1999) 'Influence of environmental stimuli on nest building and farrowing behaviour in domestic sows', *Applied Animal Behaviour Science*, 63: 131–44.

Thomas, C. D., Cameron, A., Green, R. E., *et al*. (2004) 'Extinction risk from climate change', *Nature*, 427: 145–8.

Thomas, L. W., Kline, C., Duffelmeyer, J., Maclaughlin, K., and Doherty, J. G. (1986) 'The hand-rearing and social reintegration of a Californian sealion', *International Zoo Yearbook*, 24: 279–85.

Thomas, P. R. and Powell, D. M. (2006) 'Birth and simultaneous rearing of two litters in a pack of captive African wild dogs (*Lycaon pictus*)', *Zoo Biology*, 25: 461–77.

Thomas, R., Bartlett, L., Marples, N., Kelly, D., and Cuthill, I. (2004) 'Prey selection by wild birds can allow novel and conspicuous colobus morphs to spread in prey populations', *Oikos*, 106: 285–94.

Thomas, W. and Maruska, E. (1996) 'Mixed-species exhibits with mammals', in D. Kleiman, M. Allen, K. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago Press, pp. 204–11.

Thompson, C. B., Holter, J. B., Hayes, H. H., Silver, H., and Urban, W. E., Jr (1973) 'Nutrition of white-tailed deer. I: Energy requirements of fawns', *Journal of Wildlife Management*, 37: 301–11.

Thompson, K., Roberts, M., and Rall, W. (1995) 'Factors affecting pair compatibility in captive kangaroo rats, *Dipodomys heermanni*', *Zoo Biology*, 14: 317–30.

Tinbergen, N. (1963) 'On aims and methods of ethology', *Zeitschrift für Tierpsychologie*, 20: 410–33.

Todman, J. B. and Dugard, P. (2001) *Single-Case and Small-n Experimental Designs*, Mahwah, NJ: Lawrence Erlbaum Associates.

Tofield, S., Coll, R. K., Vyle, B., and Bolstad, R. (2003) 'Zoos as a source of free choice learning', *Research in Science and Technological Education*, 21: 67–99.

Toone, W. D. and Wallace, M. P. (1994) 'The extinction in the wild and reintroduction of the California condor (*Gymnogyps californianus*)', in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner (eds), *Creative Conservation: Interactive Management of Wild and Captive Animals*, London: Chapman & Hall, pp. 411–19.

Townsend, S. (2009) 'Incorporating sustainable practices for zoos and aquariums: a triple bottom line approach', *International Zoo Yearbook*, 43: 53–63.

Travis, D. (2007) 'West Nile virus in birds and mammals', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (6th edn), St Louis, MO: Saunders Elsevier, pp. 2–9.

Traylor-Holzer, K. (ed.) (2011) *PMx Users Manual, Version 1.0.*, Apple Valley, MN: IUCN SSC Conservation Breeding Specialist Group.

Traylor-Holzer, K. and Fritz, P. (1985) 'Utilization of space by adult and juvenile groups of captive chimpanzees (*Pan troglodytes*)', *Zoo Biology*, 4: 115–27.

Tribe, A. and Booth, R. (2003) 'Assessing the role of zoos in wildlife conservation', *Human Dimensions of Wildlife*, 8: 65–74.

Trivers, R. L. (1971) 'The evolution of reciprocal altruism', *Quarterly Review of Biology*, 46: 35–57.

Trivers, R. L. (1972) 'Parental investment and sexual selection', in B. Campbell (ed.), *Sexual Selection and the Descent of Man*, Chicago, IL: Aldine, pp. 35–57.

Trivers, R. L. and Willard, D. (1973) 'Natural selection of parental ability to vary the sex ratio of offspring', *Science*, 179: 90–2.

Troyer, K. (1984a) 'Diet selection and digestion in *Iguana iguana*: the importance of age and nutrient requirements', *Oecologia*, 61: 201–7.

Troyer, K. (1984b) 'Behavioral acquisition of the hindgut fermentation system by hatchling *Iguana iguana*', *Behavioral Ecology and Sociobiology*, 14: 189–93.

Tudge, C. (1992) *Last Animals at the Zoo: How Mass Extinction Can Be Stopped*, Washington, DC/London: Island Press/Hutchinson Radius.

Tunnicliffe, S. D., Lucas, A. M., and Osborne, J. (1997) 'School visits to zoos and museums: a missed educational opportunity?', *International Journal of Science Education*, 19: 1039–56.

Turley, S. K. (1999) 'Exploring the future of the traditional UK zoo', *Journal of Vacation Marketing*, 5: 340–55.

Turner, I. (2009) 'Measuring performance: environmental management systems', *International Zoo Yearbook*, 43: 82–90.

Turvey, S. T., Pitman, R. L., Taylor, B. L., *et al.* (2007) 'First human-caused extinction of a cetacean species?' *Biology Letters*, 3: 537–40.

Tyler, S. (1979) 'Time sampling: a matter of convention', *Animal Behaviour*, 27: 801–10.

U

Ullrey, D. E. (2003) 'Metabolic bone diseases', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 749–56.

UN (United Nations) (1973) *Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES)*, Washington, DC: UNEP.

UN (United Nations) (1992) 'Convention on Biodiversity (CBD)', *International Environmental Laws: Multilateral Treaties*, 992: 1–43.

V

Valutis, L. L. and Marzuluff, J. M. (1999) 'The appropriateness of puppet-rearing birds for reintroduction', *Conservation Biology*, 13: 584–91.

van der Berg, L., van der Borg, J., and van der Meer, J. (1995) *Urban Tourism: Performance and Strategies in Eight European Cities*, Aldershot: Ashgate Publishing.

van Gelder, R. (1991) 'A big pain', *Natural History*, 100: 22–7.

van Hoek, C. S. and King, C. E. (1997) 'Causation and influence of environmental enrichment on feather picking of the crimson-bellied conure (*Pyrrhura perlata perlata*)', *Zoo Biology*, 16: 161–72.

van Keulen-Kromhout, G. (1978) 'Zoo enclosures for bears: their influence on captive behaviour and reproduction', *International Zoo Yearbook*, 18: 177–86.

van Linge, J. (1992) 'How to out-zoo the zoo', *Tourism Management*, 13: 114–17.

van Oers, K., Drent, P. J., de Goede, P., and van Noordwijk, A. J. (2004) 'Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities', *Proceedings of the Royal Society Series B: Biological Sciences*, 271: 65–73.

van Praag, H., Kempermann, G., and Gage, F. H. (2000) 'Neural consequences of environmental enrichment', *Nature Reviews Neuroscience*, 1: 191–8.

Vapnek, J. and Chapman, M. (2010) *Legislative and Regulatory Options for Animal Welfare*, Rome: Food and Agriculture Organization of the United Nations.

Vargas-Ashby, H. and Pankhurst, S. (2007) 'Effects of feeding enrichment on the behaviour and welfare of captive Waldrapps (Northern bald ibis *Geronticus eremita*)', *Animal Welfare*, 16: 369–74.

Vasey, N. and Tattersall, I. (2002) *Do Ruffed Lemurs Form a Hybrid Zone? Distribution and Discovery of* Varecia*, with Systematic and Conservation Implications*, American Museum Novitate Series 3376, New York: American Museum of Natural History.

Veasey, J. (2006) 'Concepts in the care and welfare of captive elephants', *International Zoo Yearbook*, 40: 63–79.

Veasey, J. S., Waran, N. K., and Young, R. J. (1996a) 'On comparing the behaviour of zoo-housed animals with wild conspecifics as a welfare indicator', *Animal Welfare*, 5: 13–24.

Veasey, J. S., Waran, N. K., and Young, R. J. (1996b) 'On comparing the behaviour of zoo housed animals with wild conspecifics as a welfare indicator, using the giraffe (*Giraffa camelopardalis*) as a model', *Animal Welfare*, 5: 139–53.

Vehrs, K. L. (1996) 'Summary of United States wildlife regulations applicable to zoos', in D. G. Kleiman, M. E. Allen, K. V. Thompson, and S. Lumpkin (eds), *Wild Mammals in Captivity: Principles and Techniques*, Chicago, IL: University of Chicago Press, pp. 593–9.

Veissier, I. and Boissy, A. (2007) 'Stress and welfare: two complementary concepts that are intrinsically related to the animal's point of view', Physiology and Behavior, 92: 429–33.

Veltman, K. (2009) 'How can zoos import and display butterflies for educational purposes in a sustainable way?', *International Zoo Yearbook*, 43: 124–30.

Veltman, K. and van der Zanden, R. (2000) Biological control: fighting pests with pests. *De Harpij*, 19: 5–7 (in Dutch with English summary).

Verderber, S., Gardner, L., Islam, D., and Nakanishi, L. (1988) 'Elderly persons' appraisal of the zoological environment', *Environment and Behavior*, 20: 492–507.

Vevers, G. (1976) *London's Zoo*, London: Bodley Head.

Vickery, S. and Mason, G. (2004) 'Stereotypic behavior in Asiatic black and Malayan sun bears', *Zoo Biology*, 23: 409–30.

Vickery, S. S. and Mason, G. J. (2005) 'Stereotypy and perseverative responding in caged bears: further data and analyses', *Applied Animal Behaviour Science*, 91: 247–60.

Vié, J. C. (1996) 'Reproductive biology of captive Arabian oryx *Oryx leucoryx* in Saudi Arabia', *Zoo Biology*, 15: 371–81.

Vignes, S., Newman, J. D., and Roberts, R. L. (2001) 'Mealworm feeders as environmental enrichment for common marmosets', *Contemporary Topics in Laboratory Animal Science*, 40: 26–9.

Vining, J. (2003) 'The connection to other animals and caring for nature', *Research in Human Ecology*, 10: 87–99.

Visalberghi, E. and Anderson, J. (1993) 'Reasons and risks associated with manipulating captive primates' social environments', *Animal Welfare*, 212: 3–15.

Visalberghi, E. and Vitale, A. F. (1990) 'Coated nuts as an enrichment device to elicit tool use in tufted capuchins (*Cebus apella*)', *Zoo Biology*, 9: 65–71.

Visscher, N. C., Snider, R., and Stoep, G. V. (2009). 'Comparative analysis of knowledge gain between interpretive and fact-only presentations at an animal training session: an exploratory study', *Zoo Biology*, 28: 488–95.

Vogelnest, L. and Ralph, H. K. (1997) 'Chemical immobilisation of giraffe to facilitate short procedures', *Australian Veterinary Journal*, 75: 180–2.

Vohra, R., Clark, R., and Shah, N. (2008) 'A pilot study of occupational envenomations in North American zoos and aquaria', *Clinical Toxicology*, 46: 790–3.

Voipio, H. M., Nevalainen, T., Halonen, P., Hakumaki, M., and Bjork, E. (2006) 'Role of cage material, working style and hearing sensitivity in perception of animal care noise', *Laboratory Animals*, 40: 400–9.

Vonk, J. and MacDonald, S. E. (2002) 'Natural concepts in a juvenile gorilla (*Gorilla gorilla gorilla*) at three levels of abstraction', *Journal of the Experimental Analysis of Behaviour*, 78: 315–32.

W

Wagner, K. E. and Ross, S. R. (2008) 'Chimpanzee (*Pan troglodytes*) birth patterns and human presence in zoological settings', *American Journal of Primatology*, 70: 703–6.

Waiblinger, S., Boivin, X., Pedersen, V., *et al.* (2006) 'Assessing the human–animal relationship in farmed species: a critical review', *Applied Animal Behaviour Science*, 101: 185–242.

Waits, L. P., Talbot, S. L., Ward, R. H., and Shields, G. F. (1998) 'Mitochondrial DNA phylogeography of the North American brown bear and implications for conservation', *Conservation Biology*, 12: 408–17.

Waitt, C. and Buchanan-Smith, H. M. (2001) 'What time is feeding? How delays and anticipation of feeding schedules affect stump-tailed macaque behaviour', *Applied Animal Behaviour Science*, 75: 75–85.

Waitt, C., Buchanan-Smith, H. M., and Morris, K. (2002) 'The effects of caretaker–primate relationships on primates in the laboratory', *Journal of Applied Animal Welfare Science*, 5: 309–19.

Walker, J. K., Dale, A. R., Waran, N., Clarke, N., Farnworth, M., and Wemelsfelder, F. (2010) 'The assessment of emotional expression in dogs using a Free Choice Profiling methodology', *Animal Welfare,* 19, 75–84.

Walker, S. (2001) 'Africa: national legislation and licensing', in C. E. Bell (ed.), *Encyclopedia of the World's Zoos*, Chicago, IL/London: Fitzroy Dearborn, pp. 14–15.

Waller, B. M., Peirce, K., Mitchell, H., and Micheletta, J. (2012) 'Evidence of public engagement with science: visitor learning at a zoo-housed primate research centre', *PLoS One*, 7: e44680.

Walter, O., Ellis, J. A., and Bingaman Lackey, L. (2009) 'Will the EU ban on bird imports mean the demise of bird populations in European collections?', *International Zoo Yearbook*, 43: 19–28.

Ward, P. I., Mosberger, N., Kistler, C., and Fischer, O. (1998) 'The relationship between popularity and body size in zoo animals', *Conservation Biology*, 12: 1408–11.

Ward, S. and Melfi, V. (2004) 'The influence of stockmanship on the behaviour of black rhinoceros (*Diceros bicornis*)', in C. Macdonald (ed.), *Proceedings of the Sixth Annual Symposium on Zoo Research*, London: BIAZA, pp. 160–9.

Wardzynski, C., Arne, P., and Millemann, Y. (2005) 'Methods of restraint for zoo mammals', *Point Veterinaire*, 36: 46.

Warwick, C. (1990) 'Reptilian ethology in captivity: observations of some problems and an evaluation of their aetiology', *Applied Animal Behaviour Science*, 26: 1–13.

Washio, K., Misawa, S., and Ueda, S. (1989) 'Individual identification of non-human primates using DNA fingerprinting', *Primates*, 30: 217–21.

Wasser, S. K., Hunt, K. E., Brown, J. L., *et al.* (2000) 'A generalized fecal glucocorticoid assay for use in a diverse array of non-domestic mammalian and avian species', *General and Comparative Endocrinology*, 120: 260–75.

Wasserman, F. E. and Cruikshank, W. W. (1983) 'The relationship between time of feeding and aggression in a group of captive hamadryas baboons', *Primates*, 24: 432–5.

Waterhouse, M. and Waterhouse, H. (1971) 'Population density and stress in zoo monkeys', *Ecologist*, 1: 19–21.

Wathes, C. and Charles, D. (eds) (1994) *Livestock Housing*, Wallingford, Oxon: CABI Publishing.

Watson, J. B. (1928) *The Psychological Care of Infant and Child*, London: Allen.

Watson, P. F. and Holt, W. V. (2001) 'Organizational issues concerning the establishment of a genetic resource bank', in P. F. Watson and W. Holt (eds), *Cryobanking the Genetic Resource: Wildlife Conservation for the Future?*, London: Taylor & Francis, pp. 113–22.

Watters, J. V. (2009) 'Toward a predictive theory for environmental enrichment', *Zoo Biology*, 28: 609–22.

Watters, J. V. and Meehan, C. L. (2007) 'Different strokes: can managing behavioral types increase post-release success?', *Applied Animal Behaviour Science*, 102: 364–79.

Watters, J. V. and Powell, D. M. (2012) 'Measuring animal personality for use in population management in zoos: suggested methods and rationale', *Zoo Biology*, 31: 1–12.

Watters, J. V., Miller, J .T., and Sullivan, T. J. (2011) 'Note on optimizing environmental enrichment: a study of fennec fox and zoo guests', *Zoo Biology*, 30: 647–54.

Watts, J. M. and Stookey, J. M. (1999) 'Effects of restraint and branding on rates and acoustic parameters of vocalization in beef cattle', *Applied Animal Behaviour Science*, 62: 125–35.

Watts, P. C., Buley, K. R., Sanderson, S., Boardman, W., Ciofi, C., and Gibson, R. (2006) 'Parthenogenesis in Komodo dragons', *Nature*, 444: 1021–2.

Waugh, D. (1988) 'Training in zoo biology, captive breeding and conservation', *Zoo Biology*, 7: 269–80.

Wayne, R. K., Bruford, M. W., Girman, D., Rebholz, W. E. R., Sunnucks, P., and Taylor, A. C. (1994) 'Molecular genetics of endangered species', in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner (eds), *Creative Conservation: Interactive Management of Wild and Captive Animals*, London: Chapman & Hall, pp. 92–117.

WAZA (World Association of Zoos and Aquariums) (1999) *Code of Ethics*, Liebefeld-Berne: WAZA.

WAZA (World Association of Zoos and Aquariums) (2005) *Building a Future for Wildlife: The World Zoo and Aquarium Conservation Strategy*, Liebefeld-Berne: WAZA.

WAZA (World Association of Zoos and Aquariums) (2006) *Understanding Animals and Protecting Them: About the World Zoo and Aquarium Strategy*, Liebefeld-Berne: WAZA.

WAZA (World Association of Zoos and Aquariums) (2008) 'About WAZA', available online at **http://www.waza.org/home/index.php?main=home**.

WAZA (World Association of Zoos and Aquariums) (2009) *Turning the Tide: A Global Aquarium Strategy for Conservation and Sustainability*, Liebefeld-Bern: WAZA. available from **http://www.waza.org/files/webcontent/1.public_site/5.conservation/conservation_strategies/turning_the_tide/Aquarium%20strategy%20EN.pdf**.

WAZA (World Association of Zoos and Aquariums) (2010) 'Sustainability report', available online at: **http://www.waza.org/files/webcontent/1.public_site/5.conservation/environmental_sustainability/Sustainability_Report.pdf**

WAZA (World Association of Zoos and Aquariums) (2012) 'Overview of conservation projects', available online at: **www.waza.org/en/site/conservation/waza-conservation-projects/overview** (accessed 10 November 2012).

Weary, D. M., Niel, L., Flower, F. C., and Fraser, D. (2006) 'Identifying and preventing pain in animals', *Applied Animal Behaviour Science*, 100: 64–76.

Webster, J. (1994) *Animal Welfare: A Cool Eye Towards Eden*, Oxford: Blackwell Science.

Webster, J. (2006) 'Animal sentience and animal welfare: what is it to them and what is it to us?', *Applied Animal Behaviour Science*, 100: 1–3.

Wechsler, B. (1991) 'Stereotypies in polar bears', *Zoo Biology*, 10: 177–88.

Wehnelt, S., Hosie, C., Plowman, A., and Feistner, A. (2003) *Zoo Research Guidelines: Project Planning and Behavioural Observations*, London: BIAZA.

Wehnelt, S., Bird, S., and Lenihan, A. (2006) 'Chimpanzee forest exhibit at Chester Zoo', *International Zoo Yearbook*, 40: 313–22.

Wei, F., Feng, Z., Wang, Z., Zhou, A., and Hu, J. (1999) 'Use of the nutrients in bamboo by the red panda (*Ailurus fulgens*)', *Journal of Zoology*, 248: 535–41.

Weiss, E. and Wilson, S. (2003) 'The use of classical and operant conditioning in training Aldabra tortoises (*Geochelone gigantea*) for venipuncture and other husbandry issues', *Journal of Applied Animal Welfare Science*, 6: 33–8.

Weller, S. H. and Bennett, C. L. (2001) 'Twenty-four hour activity budgets and patterns of behavior in captive ocelots (*Leopardus pardalis*)', *Applied Animal Behaviour Science*, 71: 67–79.

Wells, D. L. (2005) 'A note on the influence of visitors on the behaviour and welfare of zoo-housed gorillas', *Applied Animal Behaviour Science*, 93: 13–17.

Wells, D. L. (2009) 'Sensory stimulation as environmental enrichment for captive animals: a review', *Applied Animal Behaviour Science*, 118: 1–11.

Wells, D. L. and Egli, J. M. (2004) 'The influence of olfactory enrichment on the behaviour of captive black-footed cats, *Felis nigripes*', *Applied Animal Behaviour Science*, 85: 107–19.

Wemelsfelder, F. (1999) 'The problem of animal subjectivity and its consequences for the scientific measurement of animal suffering', in F. Dolins (ed.), *Attitudes to Animals: Views in Animal Welfare*, Cambridge: Cambridge University Press, pp. 37–53.

Wemelsfelder, F. (2001) 'The inside and outside aspects of consciousness: complementary approaches to the study of animal emotion', *Animal Welfare*, 10: 129–39.

Wemelsfelder, F. (2007) 'How animals communicate quality of life: the qualitative assessment of behaviour', Animal Welfare, 16: 25–31.

Wemelsfelder, F. and Birke, L. (1997) 'Environmental challenge', in M. C. Appleby and B. O. Hughes (eds), *Animal Welfare*, Wallingford, Oxon: CABI Publishing, pp. 35–47.

Wemelsfelder, F., Hunter, T. E. A., Mendl, M. T., and Lawrence, A. B. (2001) 'Assessing the "whole animal":

a Free-Choice-Profiling approach', *Animal Behaviour*, 62: 209–20.

Wemmer, C., Rudran, R., Dallmeier, F., and Wilson, D. E. (1993) 'Training developing-country nationals is the critical ingredient to conserving global biodiversity', *BioScience*, 43: 762–67.

Wendeln, M. C., Runkle, J. R., and Kalko, E. K. V. (2000) 'Nutritional values of 14 fig species and bat feeding preferences in Panama', *Biotropica*, 32: 489–501.

Westneat, D. F. and Stewart, I. R. K. (2003) 'Extra-pair paternity in birds: causes, correlates, and conflict', *Annual Review of Ecology, Evolution, and Systematics*, 34: 365–96.

Wharton, D. (2007) 'Research by zoos', in A. Zimmerman, M. Hatchwell, L. A. Dickie, and C. West (eds), *Zoos in the 21st Century*, Cambridge: Cambridge University Press, pp. 178–91.

Wheater, R. (1995) 'World Zoo Conservation Strategy: a blueprint for zoo development', *Biodiversity and Conservation*, 4: 544–52.

Wheler, C. L. and Fa, J. E. (1995) 'Enclosure utilization and activity of round island geckos (*Phelsuma guentheri*)', *Zoo Biology*, 14: 361–9.

Whilde, J. and Marples, N. (2011) 'The behavior of a zoo-housed infant orangutan after the death of its mother', *Zoo Biology* 30: 205–11.

Whitaker, B. R. (1999) 'Preventive medicine programs for fish', in M. E. Fowler and R. E. Miller (eds), *Zoo and Wild Animal Medicine: Current Therapy* (4th edn), Philadelphia, PA: W. B. Saunders, pp. 163–81.

White, B. C., Houser, L. A., Fuller, J. A., Taylor, S., and Elliott, J. L. L. (2003) 'Activity-based exhibition of five mammalian species: evaluation of behavioral changes', *Zoo Biology*, 22: 269–85.

White, P. A. (2005) 'Maternal rank is not correlated with cub survival in the spotted hyena, *Crocuta crocuta*', *Behavioural Ecology*, 16: 606–13.

Whitehead, G. K. (1972) *Deer of the World*, London: Constable.

Whitehead, M. (1995) 'Saying it with genes, species and habitats: biodiversity education and the role of zoos', *Biodiversity and Conservation*, 4: 664–70.

Whiten, A., Goodall, J., McGrew, W. C., *et al*. (1999) 'Chimpanzee cultures', *Nature*, 399: 682–5.

Whitford, H. L. and Young, R. J. (2004) 'Trends in the captive breeding of threatened and endangered birds in British zoos, 1988–1997', *Zoo Biology*, 23: 85–9.

Whitham, J. C. and Wielebnowski, N. (2009) 'Animal-based welfare monitoring: using keeper ratings as an assessment tool', *Zoo Biology*, 28, 545–560.

Whiting, M. J., Stuart-Fox, D. M., O'Connor, D., Firth, D., Bennett, N. C., and Blomberg, S. P. (2006) 'Ultraviolet signals ultra-aggression in a lizard', *Animal Behaviour*, 72: 353–63.

Whitney, R. and Wickings, E. (1987) 'Macaques and other old world simians', in T. Poole (ed.), *The UFAW Handbook on the Care and Management of Laboratory Animals*, Harlow: Longman, pp. 599–627.

Whitworth, A. W. (2012) 'An investigation into the determining factors of zoo visitor attendances in UK zoos', *PLoS One* 7: e29839.

Wielebnowski, N. (1996) 'Reassessing the relationship between juvenile mortality and genetic monomorphism in captive cheetahs', *Zoo Biology*, 15: 353–69.

Wielebnowski, N. (1998) 'Contributions of behavioral studies to captive management and breeding of rare and endangered mammals', in T. Caro (ed.), *Behavioral Ecology and Conservation Biology*, New York: Oxford University Press, pp. 130–62.

Wielebnowski, N. (1999) 'Behavioral differences as predictors of breeding status in captive cheetahs', *Zoo Biology*, 18: 335–49.

Wielebnowski, N., Fletchall, N., Carlstead, K., Busso, J., and Brown, J. (2002) 'Non-invasive assessment of adrenal activity associated with husbandry and behavioral factors in the North American clouded leopard population', *Zoo Biology*, 21: 77–98.

Wiepkema, P. and Koolhaas, J. (1993) 'Stress and animal welfare', *Animal Welfare*, 26: 195–218.

Wiese, R., Willis, K., Lacy, R., and Ballou, J. (2003) *AZA Studbook Analysis and Population Management Handbook*, Bethesda, MD: AZA.

Wiesner, C. S. and Iben, C. (2003) 'Influence of environmental humidity and dietary protein on pyramidal growth of carapaces in African spurred tortoises (*Geochelone sulcata*)', *Journal of Animal Physiology and Animal Nutrition*, 87: 66–74.

Wiggs, R. B. and Lobprise, H. B. (1997) 'Exotic animal oral disease and dentistry', in R. B. Wiggs and H. B. Lobprise (eds), *Veterinary Dentistry: Principles and Practice*, Oxford: Blackwell, pp. 538–58.

Wilcken, J. and Lees, C. (1998) *Managing Zoo Populations: Compiling and Analysing Studbook Data*, Sydney: ARAZPA.

Wildt, D., Ellis, S., Janssens, D., and Buff, J. (2003) 'Toward more efficient reproductive science for conservation',

in W. Holt, A. Pickard, J. Rodger, and D. Wildt (eds), *Reproductive Science and Integrated Conservation*, Cambridge: Cambridge University Press, pp. 2–20.

Wilkinson, R. (2000) 'An overview of captive-management programmes and regional collection planning for parrots', *International Zoo Yearbook*, 37: 36–58.

Williams, E. S. (2003) 'Plague', in M. E. Fowler (ed.), *Zoo and Wild Animal Medicine* (3rd edn), Philadelphia, PA: Saunders Elsevier, pp. 705–9.

Williams, E. S., Yuill, T., Artois, M., Fischer, J., and Haigh, J. A. (2002) 'Emerging infectious diseases in wildlife', *OEI Scientific and Technical Review*, 21: 139–57.

Williams, L. E. and Abee, C. R. (1988) 'Aggression with mixed age–sex groups of Bolivian squirrel monkeys following single animal introductions and new group formations', *Zoo Biology*, 7: 139–45.

Williams, R. L., Porter, S. K., Hart, A. G., and Goodenough, A. E. (2012) 'The accuracy of behavioural data collected by visitors in a zoo environment. Can visitors collect meaningful data?', *International Journal of Zoology*, doi:10.1155/2012/724835.

Williams, S. E. and Hoffman, E. A. (2009) 'Minimizing genetic adaptation in captive breeding programs: a review', *Biological Conservation*, 142: 2388–400.

Willmer, P., Stone, G., and Johnston, I. (2004) *Environmental Physiology of Animals* (2nd edn), Chichester: Wiley–Blackwell.

Wilson, A. C. and Stanley Price, M. R. (1994) 'Reintroduction as a reason for captive breeding', in P. J. S. Olney, G. M. Mace, and A. T. C. Feistner (eds), *Creative Conservation: Interactive Management of Wild and Captive Animals*, London: Chapman & Hall, pp. 243–64.

Wilson, D. E. and Reeder, D. M. (eds) (2005) *Mammal Species of the World*, Baltimore, MD: Johns Hopkins University Press.

Wilson, E. O. (1975) *Sociobiology: The New Synthesis*, Cambridge, MA: Belknap Press.

Wilson, E. O. (1984) *Biophilia*, Cambridge, MA: Harvard University Press.

Wilson, E. O. (ed.) (1988) *BioDiversity*, Washington, DC: National Academy Press.

Wilson, K. A., McBride, M. F., Bode, M., and Possingham, H. P. (2005) 'Prioritizing global conservation efforts', *Nature*, 240: 337–40.

Wilson, M., Kelling, A., Poline, L., Bloomsmith, M., and Maple, T. (2003) 'Post-occupancy evaluation of Zoo

Atlanta's Giant Panda Conservation Center: staff and visitor reactions', *Zoo Biology*, 22: 365–82.

Wilson, M. L., Bloomsmith, M. A., and Maple, T. L. (2004) 'Stereotypic swaying and serum cortisol concentrations in three captive African elephants (*Loxodonta africana*)', *Animal Welfare*, 13: 39–43.

Wilson, S. C., Mitlohner, F. M., Morrow-Tesch, J., Dailey, J. W., and McGlone, J. J. (2002) 'An assessment of several potential enrichment devices for feedlot cattle', *Applied Animal Behaviour Science*, 76: 259–65.

Wilson, S. F. (1982) 'Environmental influences on the activity of captive apes', *Zoo Biology*, 115: 201–9.

WIN (Wildlife Information Network) (2008) 'Gateway to WILDPRO', available online at http://www.wildlifeinformation.org.

Winne, C., Willson, J., Andrews, K., and Reed, R. (2006) 'Efficacy of marking snakes with disposable medical cautery units', *Herpetological Review*, 31: 52–4.

Winter, Y., Lopez, J., and von Helversen, O. (2003) 'Ultraviolet vision in a bat', *Nature*, 425: 612–14.

Wishart, G. J. (2001) 'The cryopreservation of germplasm in domestic and non-domestic birds', in P. F. Watson and W. V. Holt (eds), *Cryobanking the Genetic Resource: Wildlife Conservation for the Future?*, London: Taylor & Francis, pp. 179–200.

Wojciechowski, S. (2001) 'Is enrichment still good the next day? Overcoming the challenges of providing daily enrichment to multiple animal groups in a colony-type situation', in M. Hawkins, K. E. Worley, and B. Hammond (eds), *Fifth International Conference on Environmental Enrichment*, San Diego, CA: The Shape of Enrichment, pp. 211–20.

Wolf, M. and Weissing, F. J. (2012) 'Animal personalities: consequences for ecology and evolution', *Trends in Ecology and Evolution,* 27: 452–62.

Wolf, R. and Tymitz, B. (1981) 'Studying visitor perceptions of zoo environments: a naturalistic view', *International Zoo Yearbook*, 21: 49–53.

Wolfe, B. A. (2003) 'Toxoplasmosis', in M. E. Fowler and M. E. Miller (eds), *Zoo and Wild Animal Medicine* (5th edn), Philadelphia, PA: Saunders Elsevier, pp. 745–9.

Wolters, S. and Zuberbuhler, K. (2003) 'Mixed-species associations of Diana and Campbell's monkeys: the costs and benefits of a forest phenomenon', *Behaviour*, 140: 371–85.

Wood, W. (1998) 'Interactions among environmental enrichment, viewing crowds and zoo chimpanzees', *Zoo Biology*, 17: 211–30.

Woodfine, T., Gilbert, T., and Engel, H. (2005) 'A summary of past and present initiatives for the conservation and reintroduction of addax and scimitar-horned oryx in North Africa', in B. Hiddinga (ed.), *Proceedings of the EAZA Conference*, Amsterdam: EAZA Executive Office, pp. 208–11.

Woods, G. M., Kreiss, A., Belov, K., Siddle, H. V., Obendorf, D. L., and Muller, H. K. (2007) 'The immune response of the Tasmanian devil (*Sarcophilus harrisii*) and devil facial tumor disease', *EcoHealth*, 4: 338–45.

Woolcock, D. (2000) 'Husbandry and management of kea *Nestor notabilis* at Paradise Park, Hayle', *International Zoo Yearbook*, 37: 146–52.

Woollard, S. (1998) 'The development of zoo education', *International Zoo News*, 45: 422–6.

Woollard, S. (1999) 'A review of zoo education in the United Kingdom and Ireland', *International Zoo News*, 46: 20–4.

Woollard, S. (2001) 'Teachers' evaluation of zoo education', *International Zoo News*, 48: 240–5.

Woolverton, W., Ator, N., Beardsley, P., and Carroll, M. (1989) 'Effects of environmental conditions on the psychological well-being of primates: a review of literature', *Life Sciences*, 44: 901–17.

Wormell, D., Brayshaw, M., Price, E., and Herron, S. (1996) 'Pied tamarins *Saguinus bicolor bicolor* at the Jersey Wildlife Preservation Trust: management, behaviour and reproduction', *Dodo: Journal of the Wildlife Preservation Trust*, 32: 76–97.

WRI/IUCN/UNEP/FAO/UNESCO (World Resources Institute/ The World Conservation Union/United Nations Environment Programme in consultation with the Food and Agriculture Organization and the United Nations Education, Scientific and Cultural Organization) (1992) *Global Biodiversity Strategy: Guidelines for Action to Save, Study and Use Earth's Biotic Wealth Sustainably and Equitably*, Washington, DC: WRI.

Wyatt, T. D. (2003) *Pheromones and Animal Behaviour*, Cambridge: Cambridge University Press.

X

Xiao, J., Wang, K., and Wang, D. (2005) 'Diurnal changes of behavior and respiration of Yangtze finless porpoises (*Neophocaena phocaenoides asiaeorientalis*) in captivity', *Zoo Biology*, 24: 531–41.

Xu, Y., Fang, S., and Li, Z. (2007) 'Sustainability of the South China tiger: implications of inbreeding depression and introgression', *Conservation Genetics*, 8: 1199–1207.

Y

Yalowitz, S. S. (2004) 'Evaluating visitor conservation research at the Monterey Bay Aquarium', *Curator*, 47: 283–98.

Yates, K. and Plowman, A. (2004) 'Hoof overgrowth in Hartmann's mountain zebra is a consequence of diet, substrate, and behaviour', in C. Macdonald (ed.), *Proceedings of the Sixth Annual Symposium on Zoo Research*, London: BIAZA, pp. 305–12.

Young, A. M., Hobson, E. A., Lackey, L. B., and Wright, T. F (2012) 'Survival on the ark: life-history trends in captive parrots', *Animal Conservation*, 15: 28–43.

Young, R. J. (1998) 'Behavioural studies of guenons *Cercopithecus* spp at Edinburgh Zoo', *International Zoo Yearbook*, 36: 49–56.

Young, R. J. (2003) *Environmental Enrichment for Captive Animals*, Oxford: Blackwell Science.

Young, R. J. and Cipreste, C. F. (2004) 'Applying animal learning theory: training captive animals to comply with veterinary and husbandry procedures', *Animal Welfare*, 13: 225–32.

Young , T., Finegan, E., and Brown, R. D. (2012) 'Effects of summer microclimates on behavior of lions and tigers in zoos', *International Journal of Biometeorology*, doi: 10.1007/s00484-012-0562-6 [Epub ahead of print].

Z

Zajac, A. M. and Conboy, G. A. (eds) (2012) *Veterinary Clinical Parasitology* (8th edn), Chichester: Wiley–Blackwell.

Zhang, G. Q., Swaisgood, R. R., Wei, R. P., *et al*. (2000) 'A method for encouraging maternal care in the giant panda', *Zoo Biology*, 19: 53–63.

Zidon, R., Saltz, D., Shore, L. S., and Motro, U. (2009) 'Behavioural changes, stress, and survival following reintroduction of Persian fallow deer from two breeding facilities', *Conservation Biology*, 23: 1026–35.

Ziegler, G. (1995) 'An alternative to processed meat diets: carcass feeding at Wildlife Safari', *The Shape of Enrichment*, 4: 1–5.

Ziegler, T. (2002) 'Selected mixed-species exhibits of primates in German zoological gardens', *Primate Reports*, 64: 7–71.

Zimmermann, A. (2010). The role of zoos in contributing to *in situ* conservation, in D. G. Kleiman, K. V. Thompson, and C. Kirk Baer (eds) *Wild Mammals in Captivity: Principles and Techniques for Zoo Management* (2nd edn), Chicago, IL: University of Chicago Press, pp. 281–7.

Zimmermann, A. and Wilkinson, R. (2007) 'The conservation mission in the wild: zoos as conservation NGOs?', in A. Zimmerman, M. Hatchwell, L. Dickie, and C. West (eds), *Zoos in the 21st Century: Catalysts for Conservation?*, Cambridge: Cambridge University Press, pp. 303–22.

Zimmerman, A., Hatchwell, M., Dickie, L., and West, C. (2007) *Zoos in the 21st Century: Catalysts for Conservation?*, Cambridge: Cambridge University Press.

Zimmermann, E. W., Purchase, C. F., and Fleming, I. A. (2012) 'Reducing the incidence of net cage biting and the expression of escape-related behaviors in Atlantic cod (*Gadus morhua*) with feeding and cage enrichment', *Applied Animal Behaviour Science*, 141: 71–8.

Zimmermann, M. (1986) 'Behavioural investigations of pain in animals', in I. J. H. Duncan and V. Molony (eds), *Assessing Pain in Farm Animals*, Luxembourg: Commission of the European Communities, pp. 16–27.

Zippel, K. (2005) 'Zoos play a vital role in amphibian conservation', *AmphibiaWeb*, available online at **http://amphibiaweb.org/declines/zoo/index.html**.

Zippel, K., Lacy, R., and Byers, O. (eds) (2006) *CBSG/WAZA Amphibian Ex Situ Conservation Planning Workshop Final Report*, Apple Valley, MN: IUCN/SSC Conservation Breeding Specialist Group.

Zoos Forum (2010) *Elephants in UK Zoos: Zoos Forum Review of Issues in Elephant Husbandry in the UK*, available online at **http://archive.defra.gov.uk/wildlife-pets/zoos/documents/elephant-forum-1007.pdf.**

Zoos Victoria (2012) *Zoos Victoria Annual Report 2011/2012*, Melbourne: State of Victoria, Australia.

ZSL (Zoological Society of London) Living Conservation (2005) *Annual Report of the Zoological Society of London 2004–2005*, London: ZSL.

Zuba, J. R. (2012) 'Hoof disorders in nondomestic artiodactylids', in M. Fowler and R. E. Miller (eds), *Fowler's Zoo and Wild Animal Medicine: Current Therapy* (Vol. 7), St Louis, MO: Saunders Elsevier, pp. 619–27.

This page intentionally left blank

Index

This page intentionally left blank

Plate 1.1 Knowing about your animals requires you to be able to recognize them. In birds, like this troupial *Icterus icterus*, a leg ring is often used for identification. (Photograph: Geoff Hosey)

Plate 1.2 Keepers are significant people in zoo animals' lives, particularly where they are involved in training for a show, as with this red ruffed lemur *Varecia rubra* (Photograph: Jeroen Stevens)

Plate 2.1 The 1970s saw the development of the first 'landscape immersion' exhibits in zoos, where visitors walk through the habitat, and are 'immersed' in it, rather than standing outside an enclosure looking in. This photograph shows the Masoala Rainforest Hall at Zurich Zoo, opened in 2003, where the plants, animals, temperature, humidity, and 'rainfall' represent, as closely as possible, the natural conditions in a Madagascan rainforest. (Photograph: Zurich Zoo)

Plate 2.2 The past two or three decades have seen the opening of a number of impressive new aquariums around the world, housing a very diverse range of aquatic (mostly marine) species, such as this leafy sea dragon *Phycodurus eques* at Monterey Bay Aquarium in California. (Photograph: Jeroen Stevens)

Plate 3.1 Butterfly houses are often located within larger zoos, but there are also a number of butterfly houses that exist as individual collections and, in the UK, these are defined as zoos under the Zoo Licensing Act 1981. (Photograph: (a) Brendan Walsh; (b) Kathi Herrmann).

Plate 3.2 A Pacific white-sided dolphin *Lagenorhynchus obliquidens* at Osaka Aquarium is interacting with a keeper as part of an educational presentation. There is no formal requirement under Japanese legislation for zoos to participate in visitor education, unlike in Europe where the EU Zoos Directive requires zoos in member states to engage in educational activity. (Photograph: Jeroen Stevens)

Plate 4.1 Why are male peacocks *Pavo cristatus* so gaudy? The most plausible explanation is that bright colourful plumage in a male signals to the female that he is healthy and relatively free of parasites, and therefore is a good mating partner. (Photograph: Geoff Hosey)


Plate 4.2 Interactions such as grooming are of great importance to social animals and can even occur between different species in mixed-species exhibits, as between these black crested mangabeys *Lophocebus aterrimus* and a Western lowland gorilla *Gorilla gorilla gorilla* at Gaia Park, Netherlands. (Photograph: Tjerk ter Meulen)

Plate 5.1 Accurate animal identification is essential for captive management of zoo animals and facilitates daily monitoring of individuals; which is an essential part of ensuring good animal welfare. These photographs show (a) a leg ring in a Caribbean flamingo *Phoenicopterus ruber*, and (b) ear tags in dorcas gazelles *Gazella dorcas* (Photographs: (a) Vicky Melfi; (b) Geoff Hosey)
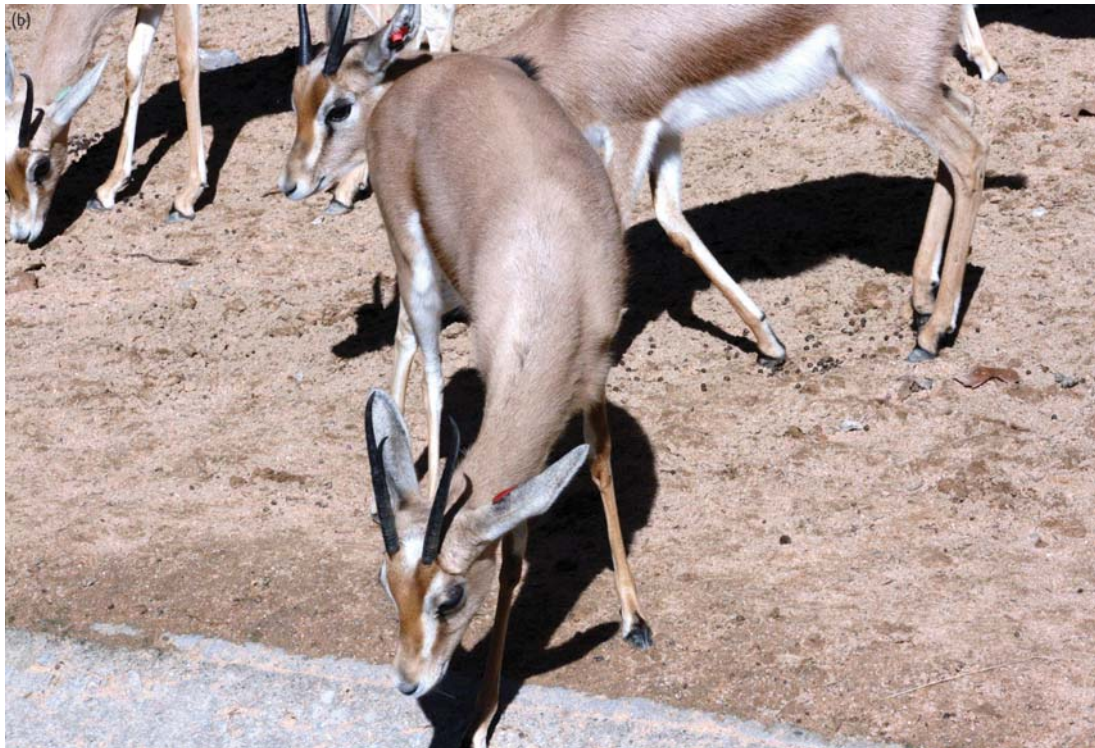
Plate 6.1 Evidence-based captive animal management should be integral to all operations in a zoo, to ensure that we make informed decisions about the lives of the animals in our care. Detroit Zoo opened this large aquatic and terrestrial habitat for two polar bears and, in an adjoining pool, seals. To determine the impact of this enclosure, and especially the 'neighbours', be they human (a) or not (b), post-occupancy evaluations could be carried out to collect evidence, as part of an evidence-based framework. (Photographs: Vicky Melfi)

Plate 7.1 Grooming is a natural and necessary behaviour, but it can develop into a problem when a bird over-grooms either itself or a companion bird. When grooming results in damage, either through feather loss or injury, it is often referred to as feather-plucking or pecking. It is uncertain what factors result in this behaviour, but it seems likely that birds, such as the Sunda wrinkled hornbill *Aceros corrugatus* pictured here, which live without behavioural restriction are unlikely to develop this behaviour. (Photograph: Ray Wiltshire, Paignton Zoo Environmental Park)

Plate 7.2 Oral stereotypy in giraffes, as in horses, is likely to reduce animal welfare. Zoo professionals work to prevent its development by providing appropriate housing and husbandry. As there are so many suggested reasons why this behaviour develops, it is important to adopt an evidence-based approach to the housing and husbandry implemented. (Photograph: Jeroen Stevens)

Plate 8.1 Challenge can be good! Much environmental enrichment is based on challenging some aspect of the animal's biology; as long as the animal has the means to cope with the challenge. But any aspect of the animal can be challenged, which means that a variety of enrichments can be provided to all animals in zoos and aquariums, and do not necessarily have to be complex. Here, the provision of what looks like a rag seems to be engaging this Californian sealion *Zalophus californianus*. (Photograph: Jeroen Stevens, Artis Zoo, Amsterdam).

Plate 9.1 Sexual dimorphism is a term used to describe morphological differences between sexes. Common characteristics of sexual dimorphism are differences in colour and size, and often it is the male of the species that is more colourful and larger, as seen here in the mandrills *Mandrillus sphinx*, among which the male (a) is more highly coloured than the female (b). (Photographs: (a) Tibor Jäger, Ramat Gan; (b) Ray Wiltshire)

Plate 9.2 Colouration of infants serves to keep them safe either by making the infant conspicuous or camouflaged. While vulnerable these primate offspring are differently coloured to their parents, (a) pink baby Sulawesi crested black macaque *Macaca nigra* and (b) white Eastern black and white colobus monkey *Colobus polykomos*. Whereas for many hoofstock, like this (c) Brazilian tapir *Tapirus terrestris*, it serves to be hidden. (Photographs: (a) and (b) Ray Wiltshire; (c) Vicky Melfi)

Plate 10.1 The blue poison dart frog *Dendrobates azureus* is one of a number of amphibian species, the survival of which currently depends on captive management efforts. (Photograph: Geoff Hosey)

Plate 10.2 Golden lion tamarins *Leontopithecus rosalia* have been the focus of one of the best-known reintroduction programmes. A successfully managed captive management programme, initiated by the Smithsonian's National Zoo, led to the propagation of a captive population and the subsequent reintroduction of animals back into their native Atlantic Coast rainforest of Brazil. (Photograph: Geoff Hosey)

Plate 11.1 Regular monitoring of the weight and body condition of zoo animals is another important part of preventive medicine. Weight change can be a sign of disease, but can also occur for a variety of other reasons, such as a change in reproductive status or seasonal patterns of fat deposition, or simply as a result of over-feeding, which is undesirable because obesity can contribute to other health problems. This photograph shows a ringtail possum *Pseudocheirus peregrinus* being weighed at Taronga Zoo in Sydney. (Photograph: Kathi Herrmann)

Plate 11.2 Vaccination is one of a range of measures that zoos can use in preventive medicine, although it is not used widely in zoos because of the possible risks associated with the use of live modified vaccines. However, the use of killed or inactivated versions of domestic cat vaccines is now fairly standard for large cats, such as lions and tigers, in zoos. This photograph shows the routine vaccination of a lion cub at Ramat Gan Zoo in Israel. (Photograph: Tibor Jäger, Zoological Center, Tel Aviv)

Plate 12.1 Even if whole carcasses cannot be provided, feeding meat on the bone rather than only meat, or meat-based products, is beneficial to the health of zoo animals. Here, a lion cub and adult male lion *Panthera leo* feed on meat on the bone at Ramat Gan Zoo, Tel Aviv, Israel. (Photograph: Tibor Jäger, Zoological Center, Tel Aviv)

Plate 12.2 Provision of browse as part of the diet is important for the health of a number of species in captivity, such as giraffes *Giraffa* spp. Giraffe skeletons contain a high proportion of calcium (Mitchell *et al.* 2006) and they appear to meet this calcium requirement by selective consumption, when available, of calcium-rich dicotyledonous browse, such as shown here. (Photograph: Liam Kite).

Plate 13.1 Opportunities for inter-specific interaction which can arise from close encounters between zoo animals and visitors are probably very enriching for the visitors, but it is unclear whether they are also enriching for the animals. Here visitors at Taronga Western Plains Zoo are able to feed browse to the giraffes. (Photograph: Geoff Hosey)

Plate 13.2 When the same keepers and animals have a long history of positive interactions with each other, it is likely that close bonds are set up between them. Here a keeper at Nagoya Aquarium has a close interaction with a beluga *Delphinapterus leucas*. (Photograph: Jeroen Stevens)

Plate 14.1 These Owston's palm civets *Chrotogale owstoni* at Newquay Zoo are part of a conservation project involving South East Asian fauna. Like so many species, they have hardly been studied, either in the wild or in captivity, and yet zoo animals like these provide relatively easy access to species which are very difficult to study in the wild. (Photograph: Geoff Hosey)

Plate 14.2 Research undertaken by students, as here at Antwerp Zoo, may generate new publishable data, but is usually regarded as more important for its role in research training. (Photograph: Jeroen Stevens)

Plate 15.1 Perhaps the zoos of the future will feature more extinct animals! Dinosaurs, seen here on tour in the community, at least have fewer husbandry and welfare needs than the living collection. (Photograph: Taronga Conservation Society Australia)

Plate 15.2 Two of a series of buttons—merchandise accompanying the Nura Diya Aboriginal Wildlife Experience at Taronga Zoo, a way of showing the continent's wildlife from an indigenous perspective (Taronga Conservation Society Australia)

ACTIVITY & EMISSIONS MAPPING
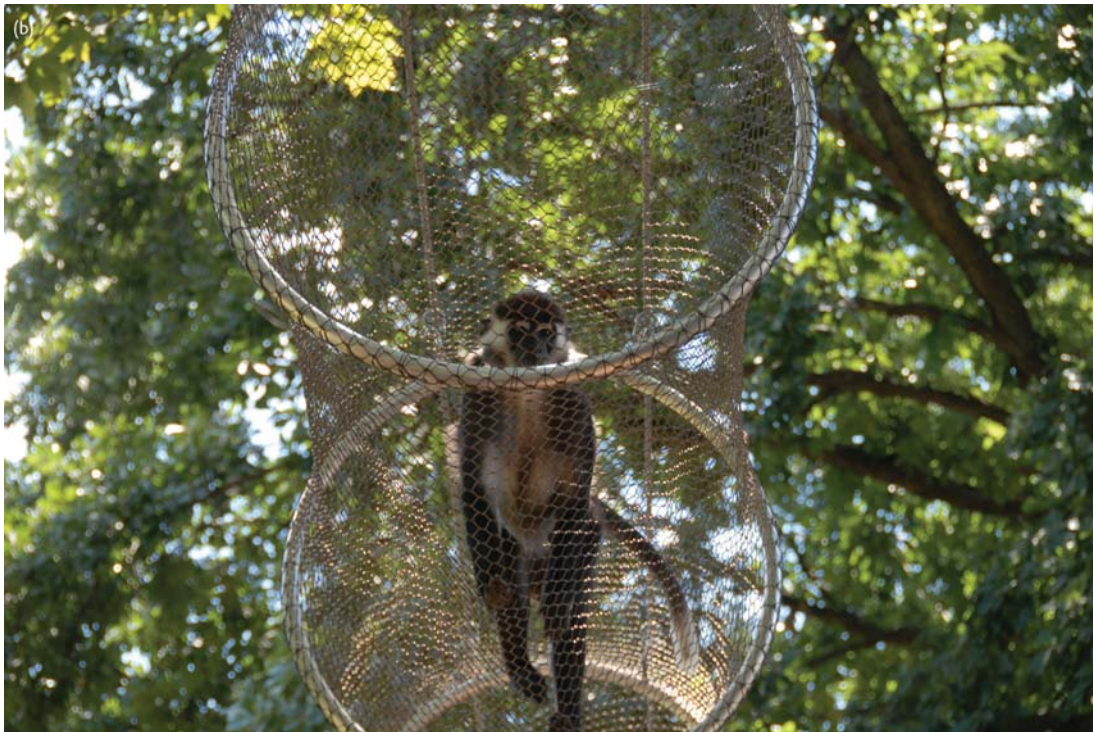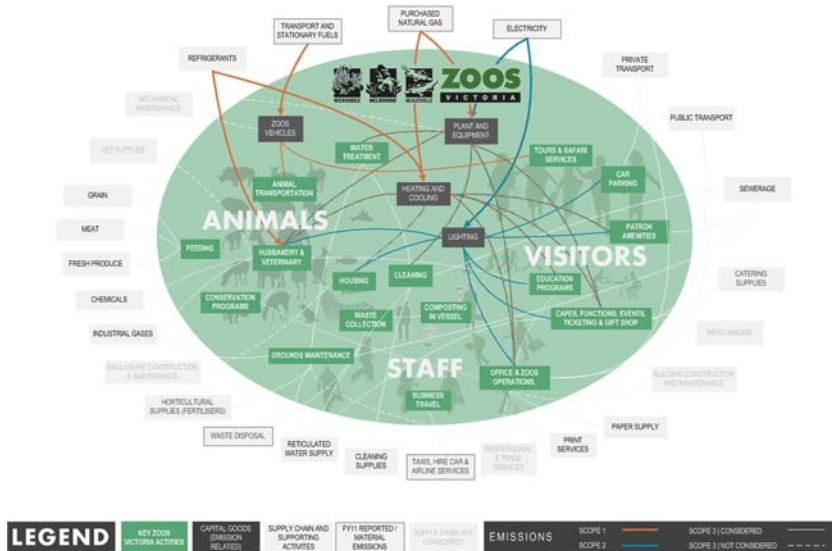
Plate 16.1 A common thread, which has hopefully become apparent during this book, is that zoos are constantly improving and progressing, and the need to be sustainable organizations is being taken increasingly seriously. For example, Zoos Victoria not only considers the environmental impact of exhibiting animals, but how its staff work and its visitors arrive at the zoo ((a); and Chapter 15). Some zoos are thinking completely outside the box, or exhibit, in terms of revolutionizing ideas on how to house animals. For example, Philadelphia Zoo is in the process of providing many of its animals, such as this red-capped mangabey *Cercocebus torquatus torquatus* (b), with the opportunity to roam, using corridors which criss-cross the zoo. (Photographs: (a): Zoos Victoria; (b): Philadelphia Zoo).